ABSTRACT

Title of Document:	VARIABLE FEMALE PREFERENCES AND THE EVOLUTION OF COMPLEX MALE DISPLAYS IN THE SATIN BOWERBIRD (*Ptilonorhynchus violaceus*)
	Seth William Coleman, Doctor of Philosophy, 2005
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Models of sexual selection suggest that females benefit from assessing male display traits to choose their mates, but little is known about how individual females use particular male traits in mate choice. Here I show age-specific use of male display traits by female satin bowerbirds. Male satin bowerbirds build specialized stick structures – bowers – for courtship and copulation, and decorate their bowers with objects collected from the environment. When a female arrives at a bower for courtship, males produce intense behavioral displays that can threaten females. Using a decoration augmentation experiment, I find that young females emphasize blue decorations in mate choice decisions, while old females emphasize male display intensity. These variable preferences support a novel hypothesis for the evolution of multiple male display traits. I find that age-specific preferences reflect age-related differences in female tolerance for intense male displays: young females do not tolerate high-intensity displays and are frequently startled during courtship, while old females actively solicit high-intensity displays, and are rarely startled by these displays. I find that the presence of blue decorations calms females, especially young females, though the reason for the calming effect remains unclear. I find age-related

improvement in females' abilities to discriminate among males in mate choice resulting in young females choosing males with higher parasite loads than those males chosen by old females. Finally, I find that juvenile males assess the quality of adult male tutors' displays when deciding which adult males to visit for male-male courtship – the behavioral context in which young males learn their displays. This finding supports a novel hypothesis for display trait learning, and shows that juvenile males have evolved preferences used in tutor choice that parallel female mate choice preferences. Overall, my work shows that (i) multiple male display traits may evolve via variable female preferences, (ii) variable female preferences may reflect interactions between female psychology and the male display traits available for assessment, and (iii) preferences for exaggerated male display traits may be shared by both sexes, but expressed in sex-specific roles.

VARIABLE FEMALE PREFERENCES AND THE EVOLUTION OF COMPLEX MALE DISPLAYS IN THE SATIN BOWERBIRD (*Ptilonorhynchus violaceus*)

By

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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2005

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Preface

This dissertation contains a single introduction section and five chapters. Chapter I is presented in the format in which it was published (*Nature*. 2004. 428, 742-745), with the introduction, results, and discussion combined in a single 'main text' section followed by the methods section, figure captions and figures, and table titles and tables at the end. Chapters II, III, and IV are presented in manuscript form, with introduction, methods, results and discussion sections, followed by table titles and table (Chapters II and IV), and figure captions and figures. Chapter V is presented in manuscript form with a single combined results and discussion section. A single bibliography section is at the end for references cited throughout the dissertation.

To Rachel, for everything.

To Sarah, for escape.

Acknowledgements

Thank you to my advisor, Dr. Gerald Borgia, for guidance throughout my dissertation, and for the opportunity to work on such an ideal system. Thanks to my committee members – Jerry, Kerry, Bob, and Dave – for their consideration and for comments on improving my work. Thanks also to Dr. Mary Christman for much statistical advice. Thank you to Al Uy and Gail Patricelli for friendship and mentoring. For helping me navigate through graduate school, I thank Lois Reid, Karen Speorl, and Sandy Davis. For friendship, thanks to the graduate students in the BEES Program and the Department of Biology.

Thanks to the Kennedy, Bell, Mulkay and Veneris families for hospitality while working in Australia. Thanks also to the field crews whose extraordinary effort made this research successful.

Thanks especially to my family: Rachel and Sarah Coleman, William and Mary Lynn Coleman, Ben, Jasmina, Natalie, and Emilie Coleman, and Emery and Marguerite Wilson. In loving memory of Frank and Virginia Coleman.

My research was financially supported by the National Science Foundation (grants to G. Borgia), and through fellowships from the Behavior, Ecology, Evolution, and Systematics Program, and the Center for Comparative and Evolutionary Biology of Hearing.

Table of Contents

List of Tables

List of Figures

INTRODUCTION

Since Darwin (1871) first developed his ideas on sexual selection, biologists have debated the evolution of extreme, sex-limited display traits. These display traits have evolved multiple times among many taxa, but the most elaborate display traits are found in species with lek-like mating systems (Andersson 1994; Höglund & Alatalo 1995). Males with extreme displays typically provide nothing to females except sperm, yet females often show strong preferences for a limited set of males (Andersson 1994; Höglund & Alatalo 1995). The issue of how exaggerated traits evolve remains controversial (see, Andersson 1994; Ryan & Rand 1993). Most discussion of sexual selection by female mate choice has focused on Fisherian 'runaway' (e.g. Fisher 1930; Lande 1981; Kirkpatrick 1985; Pomiankowski & Iwasa 1994) and 'good genes' ('indicator') models (Fisher 1915; Borgia 1979; Maynard Smith 1987; Pominakowski 1987a, b). Although neither model has gained overwhelming support, recent studies have supported predictions of different versions of good genes models (Borgia 1985a, b; Zuk et al. 1990a, b; Hill 1991; Petrie 1994; Hasselquist et al. 1996; von Schantz et al. 1996; Wilkinson et al. 1998; Jennions et al. 2001; Nowicki et al. 2002; Evans et al. 2004; Hill et al. 2005), while other studies have claimed support for runaway (Prum 1990; Møller & Pomiankowski 1993). Other important models for the evolution of elaborated display traits include sensory drive (Endler 1992), pre-existing female preference (Ryan et al. 1990), and pre-existing male trait (Borgia & Coleman 2000).

Until recently, evolutionary modelers (Lande 1981; Arnold 1983) portrayed the evolution of exaggerated display traits as the elaboration of a single trait. More recent models (Dale & Slagsvold 1996; Iwasa & Pomiankowski 1994) and empirical studies (Andersson 1989; Borgia 1985b; Borgia 1995a; Borgia & Presgraves 1998; Brooks & Couldridge 1999; Gibson et al. 1991; Kodric-Brown & Nicoleto 2001; Coleman et al. 2004) have shown that elaborate sexual displays are often complex sets of traits. However, there is little empirical data evaluating how multiple traits are used by females during mate assessment (but see, Zuk et al. 1990, 1992; Andersson 1991; Borgia 1995a; Kodric-Brown & Nicoletto 2001). This gap limits our ability to make predictions about evolutionary changes in preferences and preferred traits (Widemo & Sæther 1999), and therefore limits our understanding of evolution by sexual selection.

There are several general hypotheses that might explain the current function of multiple sexual display traits that females use in mate choice. These include: (i) multiple traits allow more accurate mate assessment by providing information about a single aspect of male quality ('redundant signal hypothesis', Møller & Pomiankowski 1993; Johnstone 1996), (ii) each display trait conveys information about different aspects of male quality ('multiple message', Møller & Pomiankowski 1993; Johnstone 1996), (iii) multiple traits function sequentially in mate assessment ('sequential signal', Borgia 1995), or (iv) multiple signals do not provide information to females regarding male quality ('unreliable indicators', Møller & Pomiankowski 1993). Currently, there is no consensus on which of these hypotheses best explains

the function of multiple traits and few studies have tested the alternatives (e.g. Andersson 1994; Candolin 2005).

While empirical tests of mate searching models are rare (but see, Forsgren 1997; Moore & Moore 1994; Uy et al. 2000, 2001a, b), anecdotal evidence suggests that female mate choice in many species is a complex process where females sample multiple males prior to choosing a single male as a mate (reviewed in, Gibson & Langen 1996). Thus, female mate choice in many species may require females to use rather sophisticated methods of discrimination in order to choose the best males as mates. My dissertation research uses the satin bowerbird (*Ptilonorhynchus violaceus*) as a model system for investigating how individual females use particular male display traits throughout the mate choice process.

Satin bowerbirds are ideal for detailed studies of female mate choice and the function of male display traits. This species has a lek-like mating system, where typical females sample multiple males in multiple courtships prior to choosing a single male as a mate (Uy et al. 2000, 2001a, b; Coleman et al. 2004). Male display sites are widely separated in the forest (> 100 m) which forces females to sample males individually – this spacing eliminates the confounding factor of simultaneous assessment of multiple males which may occur at traditional leks (Höglund & Alatolo 1995). The use of automatic video cameras at each male's display site, and intensive marking of individual birds over many years, allows me to determine which males each female samples and in what order, and which males are chosen as mates (Uy et al. 2000, 2001a, b; Coleman et al. 2004). Male satin bowerbirds provide no parental care and do not associate with females after mating, thus they are not choosy about

mates and the variance in male mating success is extreme with only a handful of males earning the majority of the matings (Borgia 1985).

Male satin bowerbirds have complex sexual displays comprised of multiple exaggerated display traits that females may use in mate choice. Males build specialized stick structures, called bowers, where courtship and copulation take place. Males decorate the areas around their bowers with various objects collected from the environment, such as feathers, flowers, snail shells, leaves, and brightly-colored artificial objects (Marshall 1954; Borgia 1985; Hunter & Dwyer 1997). Males prefer to decorate with blue objects (Borgia et al. 1987), and females prefer males with the largest numbers of blue decorations as mates (Borgia 1985; Coleman et al. 2004). Females arrive at bowers individually, thus mate choice copying is unlikely (S. W. Coleman, J. A. C. Uy and G. Borgia, unpublished data). When a female arrives at a bower for courtship, she hops into the bower, and the male begins his courtship display. These displays are intense and can threaten females during courtship, causing them to startle (Patricelli et al. 2002). To ameliorate the threat of intense displays, females signal the level of display intensity they will tolerate by 'crouching' – exaggerated movements forward and downward (Patricelli et al. 2002, 2004). A female that is crouched low to the ground signals she will tolerate a high-intensity display, while a female standing erect (not crouching at all) signals she will not tolerate a high-intensity display, and may startle in response to even low-intensity displays (Patricelli et al. 2002, 2004). Successful males must modulate their display intensity in response to female crouching (Patricelli et al. 2002). Previous work on

satin bowerbirds has shown that females vary in their tolerance for intense displays with age and experience as likely causes (Patricelli et al. 2003, 2004).

In satin bowerbirds, female mate choice is a complex process where female sample multiple males in multiple courtships through sequential mate choice stages prior to choosing a single male as a mate (Uy et al. 2000, 2001a, b; Coleman et al. 2004). During mate choice, an average female samples three males, and engages in eight courtships over fifteen days (S. W. Coleman unpub. data). Uy et al. (2000) showed that they sample males in distinct and sequential stages. Prior to building their nests, females sample multiple males in multiple "pre-nest building courtships" (Uy et al. 2000; Coleman et al. 2004). Immediately after this stage of mate choice, females spend approximately one week building their nests. After completing their nests, females return to a subset of the males initially sampled for the stage of "post-nest building courtships" (Uy et al. 2000; Coleman et al. 2004). From these subsets each female typically chooses a single male as a mate (Uy et al. 2000, 2001b; Coleman et al. 2004). The reasons females sample males in sequential stages, and whether there are differences in the sampling behaviors among stages is unclear. The objective of my work is to examine how individual females use particular male displays traits in each stage of mate choice.

In Chapter I, I use a decoration augmentation experiment to evaluate how individual females use particular male display traits in each stage of mate choice. In 1999 and 2000, I augment the number of blue decorations at half of the males' bowers in the study population, I separate females by age, and I monitor the effect on female mate choice behaviors throughout the mate choice process. I find that female

mate choice is a three-stage process: prior to observing males in pre-nest building courtships, most females (80% in 1999; 77% in 2000) visit males' bowers while the bower-owning males are absent. I find that females use these visits to assess males: females of all ages preferentially return for pre-nest building courtships to males with augmented blue decorations ('experimental males') than return to males whose blue decorations are unaugmented ('control males'). I also find that first- and second-year females continue to emphasize blue decorations in pre-nest building courtships: first- and second-year females preferentially returned to experimental males for post-nest building courtships. In contrast, the decoration augmentation had no effect on the return rates of females with three or more years of mating experience ('three-plus females'). First- and second-year females also emphasized blue decorations in the final mate choice decision: first- and second-year females preferred experimental males as mates. In contrast, three-plus females did not prefer experimental males as mates. Multiple regression analyses reveal that three-plus females emphasize male display intensity in their mate choice decisions. These results show age-specific variation in female preferences. I propose that variable female preferences provide a novel explanation for the evolution of multiple male display traits.

In Chapter II, I test the hypothesis that age-specific use of male display traits reflects age-related differences in female tolerance for intense male displays. I find under natural conditions – in 2001 with no decoration augmentation – an age-related increase in female solicitation of high-intensity male displays and an age-related decrease in the frequency that females were startled by these displays; in response, males display more intensely to old females than to young females. I also find that

frequent female startling increases the number of males sampled and the number of courtships initiated prior to choosing mates. This suggests that frequent startling may be costly, and therefore selection should favor females who learn to use intense male displays early in life. Consistent with this hypothesis, I find that by year four, females are significantly less threatened by intense male displays than are first-, second-, and third-year females. These findings suggest that variable female preferences are adaptive because they allow females to reduce mate choice costs and increase mate choice benefits.

In Chapter III, I show that under natural conditions in 2001 the ability to discriminate among males depends on female age and the male display traits used in mate choice. I find that most females, regardless of age, prefer males with above-average numbers of blue decorations and above-average display intensity as mates. I also find, however, that age-specific use of male display traits (i.e. Chapter I) resulted in older females choosing males with fewer parasites than the males chosen as mate by younger females. In Chapter II I show that females require several years of mating experience to use intense male displays in mate choice decisions. The findings of Chapter III suggest that until then, females are unable to garner the full benefits of mate choice. While it is widely appreciated that young males in many species refine their displays prior to using them to attract females, this is the first study to show that females may also require extensive experience to refine their sexual preferences. Preference refinement is adaptive because it facilitates discrimination which increases the quality of males chosen as mates.

In Chapter IV, I test the hypothesis that blue decorations calm females during courtship (see, Patricelli et al. 2003). Consistent with this hypothesis, I find that (i) females startle less frequently in courtships with experimental males than in courtships with control males, and that the calming effect of blue decorations is especially important in courtships with young females, (ii) females of all ages remain longer in courtships with experimental males than in courtships with control males, and (iii) experimental males are more attractive than control males to first- and second-year females, but not to older females. These results support the hypothesis that bower decorations reduce the threat of intense male displays, especially to young females, and facilitate female mate assessment. Selection for threat-reducing traits that co-occur with males' intense courtship displays may help to explain the widespread occurrence of multifaceted male displays.

In Chapter V, I investigate behaviors associated with the acquisition and refinement of male display traits. While the importance of adult male tutors for song learning in socially-monogamous songbirds is widely appreciated (reviewed in, Catchpole & Slater 1995), the role of display trait tutors in species with lek-like mating systems remains unclear. I propose that in these species, sexual selection may favor the evolution of juvenile males' tutor preferences that facilitate the acquisition of high quality sexual displays. To test this hypothesis, I experimentally-augment adult male satin bowerbirds' displays, and evaluate juvenile male display trait acquisition behaviors. I find that juvenile males preferentially observe the displays of adult males that, (i) have augmented blue bower decorations, (ii) have the most intense behavioral displays, and (iii) are most often chosen by females as mates.

These preferences parallel female preferences used in mate choice. Using tutor preferences that parallel female mate choice preferences allows young males to identify attractive tutors without having to evolve preferences *de novo*. I suggest tutor preferences that parallel female mate choice preferences are widespread in polygynous species where young males acquire displays by observing adult males, and where females choose mates based on the quality of sexual displays.

CHAPTER I

Variable female preferences drive complex male displays

ABSTRACT

Complexity in male sexual displays is widely appreciated but diversity in female mate choice has received relatively little attention. Males of many species have sexual displays composed of multiple display traits and females are thought to use these different traits in mate choice. Models of multiple display trait evolution suggest that these traits provide females different kinds of information in different stages of the mate choice process or function as redundant signals to improve the accuracy of mate assessment. I suggest that complex male displays could also arise because of variation in female preferences for particular male display traits. The causes of female preference variation have received little attention, and the role of preference variation in shaping complex male displays is unclear. Here I show that in satin bowerbirds (*Ptilonorhynchus violaceus*) female mate choice is a multistage process, where females of different ages use different male display traits in successive stages. Age- and stage-specific female preferences may contribute to explaining the widespread occurrence of multifaceted male displays.

MAIN TEXT

Male satin bowerbirds build specialized stick structures, called bowers, where courtship and copulation take place (Marshall 1954; Borgia 1985). Males have multiple display elements combining intense behavioral displays with bower decoration displays (Borgia 1985; Patricelli et al. 2002). Intense behavioral displays can be both attractive and threatening to females; this threat is reduced when males adjust their display in response to female signals that indicate the level of intensity the female will tolerate (Patricelli et al. 2002, 2004). Females differ in their tolerance of intense display with age/experience as a likely cause (Patricelli et al. 2004). If young, inexperienced females have a lower tolerance for intense display, then I expect them to emphasize non-threatening display elements, such as bower decorations, in their mate choice decisions. If older, more experienced females are both more tolerant of intense display and are better able to assess males using intense display, then I expect them to emphasize male display intensity in their mate choice decisions. Here I consider two questions, (i) do females show age-related differences in how they use male display traits to choose mates, and (ii) are those differences related to female tolerance of male display intensity? To test these hypotheses, I augmented the blue decorations (Figure 1) at a subset of bowers in a natural population of satin bowerbirds, separated females into age classes ('first-year females', 'second-year females', 'three-plus females' [females with 2 or more years of mating experience]), and then monitored individual female's mating-related decisions throughout the mate choice process.

In satin bowerbirds, female mate choice occurs in three stages: 'visits', 'pre-nest building courtships' (pre-NB) and 'post-nest building courtships' (post-NB) (Uy et al. 2000, 2001a, b). Prior to pre-NB courtships, most females (year 1999: 80%; year 2000: 77%) engage in a stage of 'visits' to males' bowers while the bower owners are absent; visits allowed me to evaluate the effect of blue bower decorations on female mate choice decisions independent of a male's intense courtship display. Following visits, each female engages in pre-NB courtships at the bowers of several males. During courtship, the female stands inside the bower while the male displays intensely on the platform in front of the bower (Patricelli et al. 2002). Following pre-NB courtships, each female spends approximately one week building her nest before returning for several post-NB courtships with a subset of the males previously sampled (Uy et al. 2001b). From this subset, each female typically chooses a single male as a mate. After each visit to a bower, a female has two options: (i) reject the male, or (ii) return for pre-NB courtship. After each courtship a female has three options: (i) reject the male, (ii) return for another courtship, or (iii) copulate. Detailed information on individual female's mate searching patterns allowed me to evaluate which of these options was chosen at each stage of mate choice and whether female age affected the use of blue bower decorations and male display intensity in these decisions.

In the first stage of the mate choice process, females visit males' bowers while the bower-owning males are absent. Following each visit, a female must decide whether to reject the bower-owning male from her pool of potential mates or return to him for pre-NB courtship. By evaluating the mean proportions of females that

returned to ‘experimental’ or ‘control’ males for pre-NB courtships following visits, I tested the hypothesis that females use blue decorations in the first stage of mate choice. In both 1999 and 2000, all age classes of females preferentially returned for pre-NB courtships with experimental males over control males (Figure 2a, b). These results show that females of all age classes assess blue bower decorations during visits and use the information in decisions related to returning for pre-NB courtships.

In the second stage of the mate choice process, females engage in pre-NB courtships with multiple males. During these courtships, the bower owning male is present and all elements of male display, including courtship display intensity, are available for assessment. I tested the hypothesis that blue decorations affect females’ decisions to return for post-NB courtships. Following pre-NB courtships, I found age-related differences in the proportions of females returning to experimental and control males. First- and second-year females returned preferentially to experimental males for post-NB courtships in both years, while there was no effect on the post-NB return rates of three-plus females in either year (Figure 3a, b). In both years, larger proportions of first- and second-year females than three-plus females returned to experimental males for post-NB courtships (Figure 3a, b).

After building their nests, females initiate the third stage of the mate choice process by engaging in post-NB courtships with a subset of the males sampled in pre-NB courtships (Uy et al. 2000, 2001b). From this subset, a female typically chooses a single male as a mate, and I tested the hypothesis that females prefer males with augmented blue decorations as mates. In 1999, second-year and three-plus females did not prefer experimental males as mates, while first-year females tended to prefer

experimental males as mates (Figure 4a). In 2000, I increased the number of males in the experiment and increased the number of decorations used to augment bowers (Figure 1). Again, the mate choices of three-plus females were not affected by the augmentation (Figure 4b). First- and second-year females, however, showed significant mating preferences for experimental males (Figure 4b). Among age classes in 1999, there were no differences in the proportions of females that chose experimental males as mates, while in 2000, larger proportions of first- and second-year females than three-plus females chose experimental males as mates (Table 5). Our study shows that young females emphasize blue decorations in decisions made throughout the mate choice process, while older females use blue decorations in decisions only when a male's behavioral displays are unavailable for assessment. A previous study suggested that young females are more threatened and less tolerant of intense male displays than older females (Patricelli et al. 2003), and therefore may be averse to using intense male displays in mate choice. In 2000, I tested the hypothesis that the mate choice decisions of older females are affected by male display intensity, while the decisions of younger females are not. There was no difference in mean display intensity between experimental and control males (experimental males = 39.99 ± 3.65; control males = 37.81 ± 2.56; $t_{26} = 0.49$, $P = 0.63$), therefore, I considered all males a single group for regression analyses. As predicted, display intensity did not explain a significant amount of the variation in the proportions of first-year females ($r^2 = 0.07$, $F_{1,20} = 1.67$, $P = 0.21$) or second-year females ($r^2 = 0.003$, $F_{1,12} = 0.04$, $P = 0.84$) that returned for post-NB courtships. In contrast, male display intensity explained a significant amount of the variation in the proportion of

three-plus females that returned for post-NB courtships ($r^2 = 0.38$, $F_{1,26} = 15.67$, $P < 0.01$). Comparisons of regression coefficients among age classes show that male display intensity had a larger effect on the decisions of three-plus females than younger females ($F_{2,58} = 29.30$, $P < 0.001$). These results are consistent with those from the decoration augmentation experiment: young females emphasize blue decorations throughout the mate choice process, while older females use blue decorations only when a male's behavioral display elements, such as display intensity, are unavailable for assessment. Age-related differences in females' tolerance of intense male displays (Patricelli et al. 2003) may explain the age-related reliance on different display elements in mate choice. An alternative explanation is that the differences in old and young females' use of blue decorations could result because of age-related differences in female fidelity (Uy et al. 2000, 2001a) but I found no support for this hypothesis (Table 1).

I show that mate choice in satin bowerbirds is a complex process made up of multiple stages, where females make sequential stage-specific decisions based on the assessment of male display traits, and there are age-specific differences among females in the male traits used in assessment. The differences in females' use of blue decorations versus display intensity may be related to the threatening nature of male displays. Display intensity may be a better indicator of male quality than are blue decorations (Andersson 1994; Patricelli et al. 2002, 2003), but because young females are more easily threatened by intense displays than are older females, young females may be unable to assess display intensity during mate choice. Similar age- and stage-specific female preferences may occur in the numerous other species where males

have multifaceted displays, where females sample multiple males before choosing mates, and where females choose mates based on the assessment of multiple display traits (for reviews see, Andersson 1994; Candolin 2003; Hebets & Papaj 2005). The variation in female preferences may not have been detected because detection requires experimental manipulation of male traits combined with intensive monitoring of individual females throughout the mate choice process. I suggest that as more intensive studies of mate choice are done in which intrinsic female factors (i.e. age/experience) and the stages of mate choice are considered, that variable female preferences will be discovered and may explain the widespread occurrence of multifaceted male displays.

METHODS

Marking and monitoring

This work was conducted in 1999 and 2000 at Wallaby Creek, New South Wales, Australia. Prior to the mating season, birds were captured using traps and mist nets. Each individual was fitted with three plastic leg bands arranged in a unique color-combination. In our study population, all adult males and most (1999: 87%; 2000: 91%) of the females were uniquely marked for identification. From 1 November to 20 December, automatic Hi-8 video cameras recorded behaviors at 24 (1999) and 28 (2000) adjacent bowers. This monitoring provided a complete record of all courtships

and copulations. Individuals were classified as female only if they were observed copulating with a male on videotape. Detailed mate sampling patterns and mate choice for 52 (1999) and 64 (2000) females were reconstructed from video footage.

Decoration augmentation experiment

Using information from 1998 (see, Uy et al. 2000, 2001a), bower-owning males were paired to maximize similarity in mating success (number of different mates). In 1999, the bower of one male in each dyad was randomly selected for augmentation with blue bower decorations ('experimental males'), while the other male's decorations remained unaugmented ('control males'). In 1999, 20 blue plastic tiles (2.54 cm x 2.54 cm) were placed in two arcs of 10 tiles on the bower platform of each experimental male. In 2000, I used the same males in the experimental and control groups in addition to two new experimental males, paired with two new control males. In this second year, 20 blue tiles and 50 strands of blue plastic (25cm x ~0.20cm) (Figure 5) were placed in caches 1 meter from the bower platform. Within 2 hours, each experimental male placed all of the tiles and plastic strands on his bower platform (Figure 1). Blue plastic strands are frequently used as bower decorations in the Wallaby Creek population, and the number of strands used in the augmentation was within the range of plastic strands displayed by bower owing males prior to the augmentation (mean number ± s.e. of plastic strands on bowers prior to the experiment: 45 ± 7.73) (S. W. Coleman, G. Borgia, in prep.). To prevent

decoration stealing, after experimental males placed their tiles, each tile was glued to the head of a long screw then secured into the ground. Plastic strands were frequently woven into the bower platform by bower owners, likely reducing the frequency of stealing (S. W. Coleman, G. Borgia, pers. obs.). Twice a day at each bower, the numbers of tiles and plastic strands were counted and replaced to original levels if necessary. Tiles and plastic strands found on the bowers of control males as a result of decoration stealing were removed. All other bower decorations (Borgia 1985) remained unmanipulated.

Female age classes

Females were grouped based on their years of mating experience. 'Three-plus' females had at least 2 years of prior mating experience. 'Second-year' females had 1 year of prior mating experience. 'First-year' females were not previously observed mating. All first-year females in 1999 (n = 12) and 2000 (n = 16) were captured and marked for the first time in those years. Further suggesting that these were first-year females, I found that they weighed significantly less than three-plus females (t_{65} = 2.11, $P < 0.01$). All females used in our analyses were courted by at least one experimental male and one control male.

Male display intensity

Intense male displays involve loud buzzing vocalizations, ptiloerection, and vigorous running across the bower platform with wings extended, all performed in close proximity to the female (Patricelli et al. 2002, 2003), followed by mimicry of local species (Loffredo & Borgia 1986). Females are 2.7 times more likely to be startled during the intense portion of courtship than in the remainder of courtship, even though intense elements represent an average of only 17% of the courtship duration (Patricelli et al. 2003), thus I focus on intense elements in this study.

For each intense element, I quantified three highly variable aspects of display intensity which affect the level of threat to females (Patricelli et al. 2002). The distance run by the male during the display was measured relative to the width of a bower on a scale of 1 to 6 (1 is no movement, 6 is two average bower-widths, or 40 cm). The degree that the male erects his feathers, making him appear larger, was scored on a scale of 1 to 6 (1 is not erected, 6 is fully erected). The location of the male on the bower platform was scored on a scale of 1 to 6 (1 is farthest from the female, 6 is closest to the female). Higher scores indicate more intense displays for all 3 variables. Since males may alter any combination of the distance, ptiloerection and area variables in response to female signals, scores for the variables were multiplied to calculate the intensity of each intense element (results were qualitatively the same when intensity was calculated additively). For each male, I calculated display intensity in the first pre-NB courtship with each courted female in 2000; and, for each male I calculated mean display intensity, and used these means in regression analyses

to evaluate the relative contribution of display intensity to the proportions of females returning for post-NB courtships.

Statistical analyses

For statistical analyses, I used SAS and Statistica (Version 6). I used Student's t-tests for pairwise comparisons of mean proportions of females that returned for courtships with experimental versus control males. I used regression analyses to determine the amount of variation in female return rates that was explained by male display intensity. I used Chi-square goodness-of-fit tests to evaluate female mating preferences. All tests are two-tailed unless otherwise noted.

Figure 1. Photograph of a bower with experimentally-augmented blue decorations in 2000. 'Experimental males' placed 20 blue tiles and 50 blue plastic strands on their bower platforms; bower decorations of 'control males' remained unaugmented.

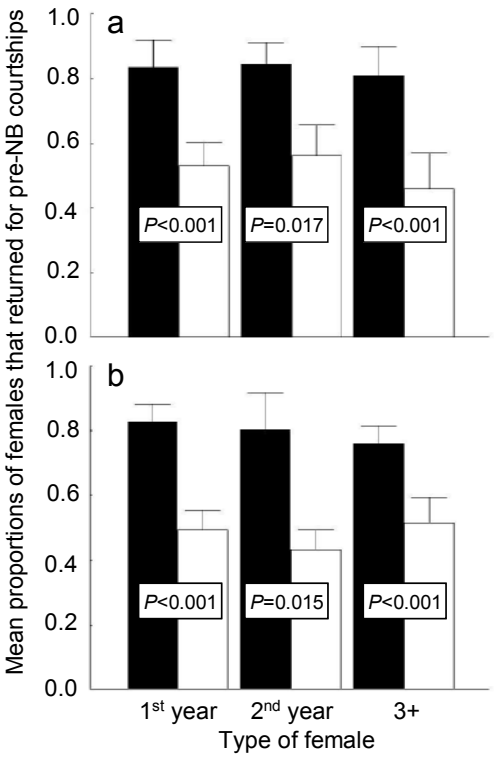
Figure 2. Mean proportions of females that returned to experimental (solid bars) or control (open bars) males for pre-NB courtships in (a) 1999 and (b) 2000. In both years, following visits all females preferentially returned to experimental males for pre-NB courtships. Bars and whiskers represent mean + s.e. *P*-values for within age class comparisons are inset. Among age classes, there were no differences in the mean proportions of females that returned to experimental males for pre-NB courtships. For complete *t*-values, df, and *P*-values, see Table 2.

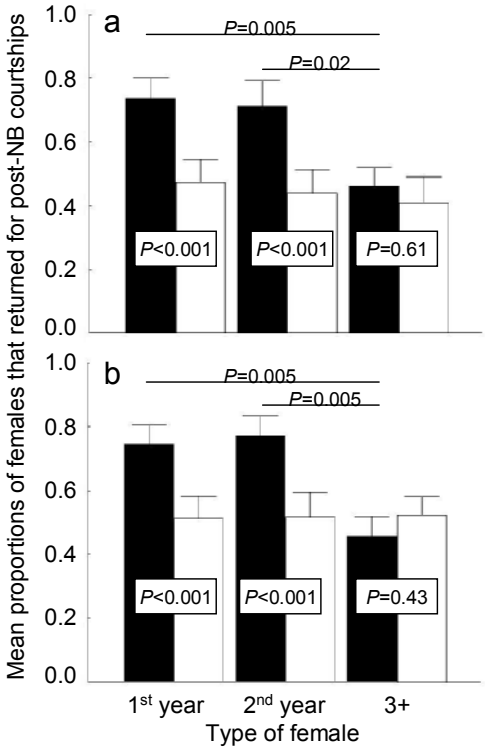
Figure 3. Mean proportions of females that returned to experimental (solid bars) or control (open bars) males for post-NB courtships in (a) 1999 and (b) 2000. In both years, following pre-NB courtships first- and second-year females preferentially returned to experimental males for post-NB courtships; three-plus females did not. Bars and whiskers represent mean + s.e. *P*-values for within age class comparisons are inset. P-values at the top of each panel indicate significant differences among age classes in the mean proportions of females that returned to experimental males for post-NB courtship. For complete *t*-values, df, and *P*-values, see Table 3.

Figure 4. Proportions of females that mated with experimental males (solid bars) or control males (open bars) in (a) 1999 and (b) 2000. In 1999, first-year females tended

to prefer experimental males as mates; second-year and three-plus females did not. In 2000, first- and second-year females preferred experimental males; three-plus females did not. *P*-values for within age class each comparison are inset. For chi-square values and df, see Table 4. For comparisons among age classes in the proportions of females that chose experimental males as mates, see Table 5. Sample sizes are above the bars.

Figure 5. Reflectance curves for the blue tiles (1999, 2000) (solid line) and blue plastic strands (2000) (broken line) used in the decoration augmentation experiment. To measure the reflectance of tiles, I used an Ocean Optics 2000 spectroradiometer and a Xenon flash light source (Ocean Optics PX-2). The scanning lens and light source came at an angle of 45 degrees. To standardize the scans, I used a > 97% spectralon (Labsphere) and a dark current reading. Scans were taken from a *ca*. 2 mm area at 0.40 nm intervals across a spectrum of 300 nm to 700 nm, which contains the visible spectrum of most avian species.


a
b
1.0
0.8
0.6
0.4
0.2
0.0
P<0.001
P=0.017
P<0.001
P<0.001
P=0.015
P<0.001
Mean proportions of females that returned for pre-NB courtships
1st year
2nd year
3+
Type of female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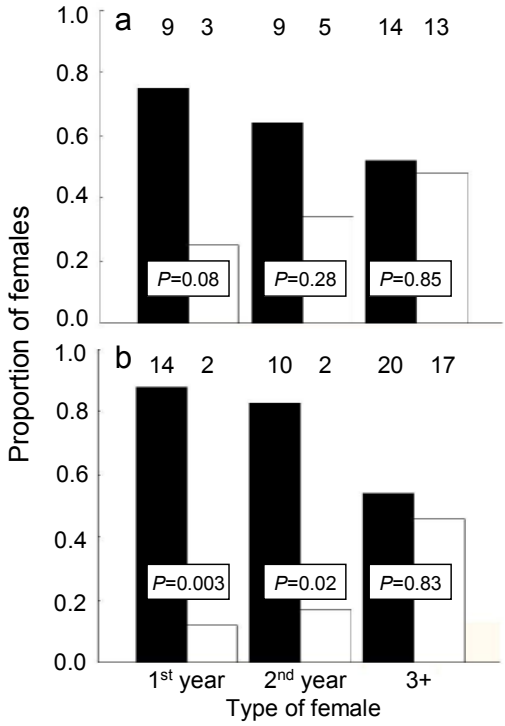
P=0.005
P=0.02
P<0.001
P<0.001
P=0.61
b
P=0.005
P=0.005
P<0.001
P<0.001
P=0.43
1.0
0.8
0.6
0.4
0.2
0.0
Mean proportions of females that returned for post-NB courtships
1st year
2nd year
3+
Type of female


a
9 3
9 5
14 13
P=0.08
P=0.28
P=0.85
b
14 2
10 2
20 17
P=0.003
P=0.02
P=0.83
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of females
1st year
2nd year
3+
Type of female

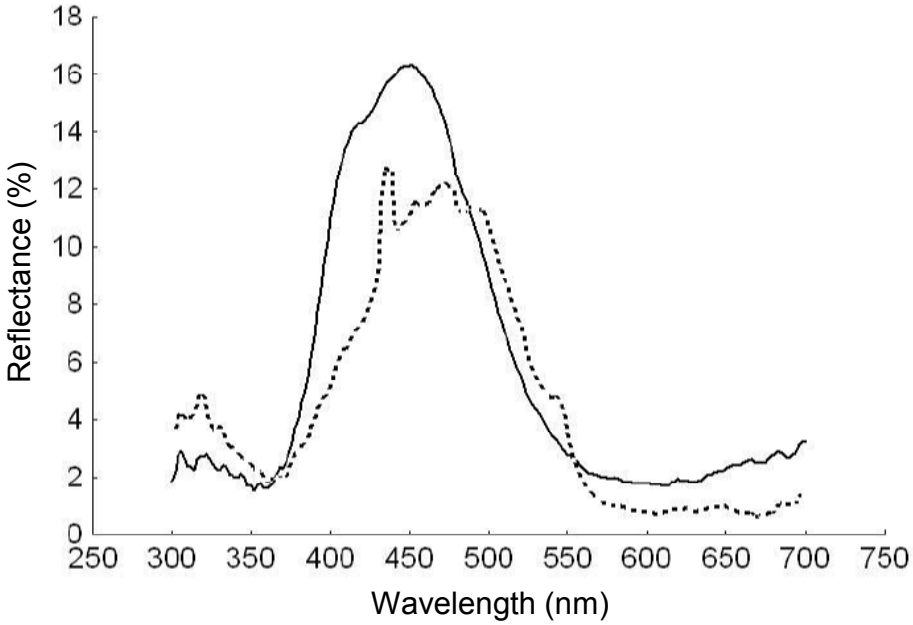

Reflectance (%)
Wavelength (nm)
0
2
4
6
8
10
12
14
16
18
250
300
350
400
450
500
550
600
650
700
750

Table 1. Effects of the decoration augmentation experiment on the mate choices of females that re-mated with mates from 1999, or switched mates between 1999 and 2000. I tested the hypothesis that the lack of effect of the decoration augmentation on the mate choices of three-plus females was due to differences in female fidelity. To test this hypothesis, I separated females into two groups: (i) females that were faithful to their previous mates, and (ii) females that switched mates between 1999 and 2000. Altogether, these results show that the addition of blue decorations did not affect mate fidelity (i.e. number of females that re-mated with previous mates), and that among females that switched mates, three-plus females did not use blue decorations in choosing their new mates, while second-year females did.

Table 2. *t*-values, df, and *P*-values for comparisons within and among age classes in the mean proportions of females returning for pre-NB courtships. Within age-class comparisons show that all females in each age class preferentially returned to experimental males for pre-NB courtships. Among age class comparisons show that females of all age classes returned equally to experimental males for pre-NB courtships.

Table 3. *t*-values, df, and *P*-values for comparisons within and among age classes in the mean proportions of females returning for post-NB courtships. Within age class comparisons show that first- and second-year females preferentially returned to experimental males for post-NB courtships, while three-plus females did not. Among age class comparisons show that the

mean proportions of first- and second-year females that returned to experimental males for post-NB courtships was larger than the mean proportions of three-plus females that returned to experimental males for post-NB courtships.

Table 4. Female mating preferences for male with augmented blue bower decorations. This table shows the comparisons of the observed (obs) and expected (exp) number of females in each age class that chose experimental males as mates.

Table 5. Comparisons among age classes of the proportions of female that chose experimental males as mates. These results show that in 2000, larger proportions of first- and second-year females chose experimental males than did three-plus females.

Table 1. Effects of the decoration augmentation experiment on the mate choices of females that re-mated with mates from 1999, or switched mates between 1999 and 2000.

Re-mated/Switched	Female age	Number of females that mated with:		X^2	df	*P*
		Experimental males	Control males			
Re-mated	Second-year	2	4	0.67	1	0.41
Re-mated	Three-plus	9	7	0.05	1	0.83
Switched	Second-year	5	0	5.00	1	0.025
Switched	Three-plus	11	10	0.25	1	0.62

Table 2. *t*-values, *df*, and *P*-values for comparisons within and among age classes in the mean proportions of females returning for pre-NB courtships.

Among/Within age class	Year	Comparison	*t*	df	*P*	Figure in Coleman et al.
Within	1999	First-year	6.04	10	<0.001	Fig. 2A
Within	1999	Second-year	3.24	7	0.017	Fig. 2A
Within	1999	Three-plus	4.49	10	<0.001	Fig. 2A
Within	2000	First-year	5.96	9	<0.001	Fig. 2B
Within	2000	Second-year	3.58	5	0.015	Fig. 2B
Within	2000	Three-plus	4.82	15	<0.001	Fig. 2B
Among	1999	First-year vs. Second-year	-0.09	9	0.92	Fig. 2A
Among	1999	First-year vs. Three-plus	0.19	10	0.84	Fig. 2A
Among	1999	Second-year vs. Three-plus	0.30	9	0.77	Fig. 2A
Among	2000	First-year vs. Second-year	0.22	6	0.83	Fig. 2B
Among	2000	First-year vs. Three-plus	0.78	20	0.44	Fig. 2B
Among	2000	Second-year vs. Three-plus	0.38	10	0.71	Fig. 2B

Table 3. *t*-values, *df*, and *P*-values for comparisons within and among age classes in the mean proportions of females returning for post-NB courtships.

Among/Within age class	Year	Comparison	*t*	df	*P*	Figure in Coleman et al.
Within	1999	First-year	6.46	18	<0.001	Fig. 3A
Within	1999	Second-year	6.59	14	<0.001	Fig. 3A
Within	1999	Three-plus	0.52	22	0.61	Fig. 3A
Within	2000	First-year	7.81	20	<0.001	Fig. 3B
Within	2000	Second-year	5.17	12	<0.001	Fig. 3B
Within	2000	Three-plus	-0.80	26	0.43	Fig. 3B
Among	1999	First-year vs. Second-year	0.25	16	0.81	Fig. 3A
Among	1999	First-year vs. Three-plus	3.17	20	0.005	Fig. 3A
Among	1999	Second-year vs. Three-plus	2.56	18	0.02	Fig. 3A
Among	2000	First-year vs. Second-year	-0.29	17	0.77	Fig. 3B
Among	2000	First-year vs. Three-plus	3.29	23	0.003	Fig. 3B
Among	2000	Second-year vs. Three-plus	3.31	20	0.003	Fig. 3B

Table 4. Female mating preferences for male with augmented blue bower decorations.

Year	Female age	Obs	Exp	X^2	df	*P*
1999	First-year	9	6	3.00	1	0.08
1999	Second-year	9	7	1.14	1	0.28
1999	Three-plus	14	13.5	0.04	1	0.85
2000	First-year	14	8	9.00	1	0.002
2000	Second-year	10	6	6.80	1	0.009
2000	Three-plus	20	18.5	0.05	1	0.83

Table 5. Comparisons among age classes of the proportions of female that chose experimental males as mates.

Year	Comparison	*z*	*P*
1999	First-year vs Second-year	0.19	0.62
1999	First-year vs Three-plus	1.10	0.11
1999	Second-year vs Three-plus	0.57	0.30
2000	First-year vs Second-year	0.31	0.44
2000	First-year vs Three-plus	2.09	0.01
2000	Second-year vs Three-plus	1.61	0.04

CHAPTER II

Variable female preferences reflect age-related differences in female tolerance for intense male displays

ABSTRACT

Females in many species accumulate extensive mating experience in their lifetimes, yet models of mate choice have not considered long-term effects of female experience. I investigated the causes and costs of age-specific female preferences in satin bowerbirds, a species where older females emphasize males' intense behavioral displays in mate choice – these displays can threaten females during courtship – while younger females emphasize non-threatening male traits in mate choice decisions. I tested the hypothesis that this age-specific use of male display traits reflects age-related differences in female tolerance for intense male displays. Supporting this hypothesis, I found (i) an age-related increase in female solicitation of high-intensity male displays, (ii) an age-related decrease in the frequency that females were startled by these displays, and (iii) that male display intensity increased as a function of female age. I also found that frequent female startling was associated with the number of males sampled and the number of courtships initiated prior to choosing mates, suggesting that frequent startling may be costly for young females. Overall, my results suggest that several years of mating experience are necessary for female satin bowerbirds to

learn to tolerate intense male displays. I suggest that in many species where males have complex sexual displays, females may require extensive mating experience to learn to use these displays in mate choice. Until then, females may emphasize a subset of male display traits in their mate choice decisions, and may not garner the full benefits of mate choice.

INTRODUCTION

Mate choice studies have often assumed uniform female preferences within species (Carson 1994; Jennions & Petrie 1997). Recent reviews of mate choice (Jennions & Petrie 1997; Widemo & Sæther 1999) indicate that in studies where preference variation was found it was assumed to be the result of constraints on females' abilities to choose mates. There is growing evidence, however, that phenotypic variation among females in mate choice is common (Partridge 1988; Ritchie 1992; Brooks & Caithness 1995; Jennions et al. 1997; Jennions & Petrie 1997; Widemo & Sæther 1999; Murphy & Gerhardt 2000; Brooks & Endler 2001; Kodric-Brown & Nicoletto 2001), and that it may be adaptive (Ryan et al. 1992; Moore & Moore 2001; Coleman et al. 2004). In cricket frogs (*Acris crepitans*), for example, small females prefer males with high-frequency mating calls while large females prefer males with low-frequency mating calls which facilitates size-assortative mating (Ryan et al. 1992). In cockroaches (*Nauphoeta cinerea*), old females are less choosey than young females which may reflect a trade-off between choosiness and senescence (Moore & Moore

2001). And in satin bowerbirds (*Ptilonorhynchus violaceus*), young females emphasize blue bower decorations – objects males use to decorate their display sites – while old females emphasize male display intensity in their mate choice decisions (Coleman et al. 2004); by switching to emphasize display intensity, old females are better than young females at choosing high-quality males as mates (Coleman 2005). These studies suggest that variable female preferences may be adaptive, and may often be related to female age or experience (see also, Burley & Moran 1979; Prosser et al. 1997; Kodric-Brown & Nicoletto 2001). However, most of this work does not explain why female preferences change as a function of female age and experience.

Coincidentally, young female guppies (*Poecilia reticulata*) and young female satin bowerbirds emphasize display trait color in mate choice decisions while old females emphasize display intensity (Kodric-Brown & Nicoletto 2001; Coleman et al. 2004). These parallel patterns suggest that similar selection pressures may contribute to preference variation in these two distinct cases. Coleman et al. (2004) suggest a hypothesis for why this occurs: young females are threatened by intense male displays and must rely on less threatening mate choice signals. They point out that several years of mating experience may be necessary for females to learn to tolerate intense male displays, but that it ultimately benefits females to use intense male displays in mate choice decisions because they are good indicators of male quality (e.g. Borgia & Presgraves 1998; Maynard Smith & Harper 2003). To test the hypothesis that variable female preferences reflect age-related differences in female tolerance for intense male displays, I follow eighty-four female satin bowerbirds from six age classes as they sample males in mate choice. I quantify male display intensity

during courtship, and female behaviors that are related to tolerance for intense male displays. My detailed analysis of male and female courtship behaviors combined with my ability to separate females by age allows me to identify the causes of female preference variation, and to assess whether preference variation is adaptive for females.

The natural population of satin bowerbirds that I work with is well suited for investigating variation in female preferences. Female satin bowerbirds can live more than twenty-seven years in the wild (G. Borgia unpub. data), mate in their first year (Coleman et al. 2004), and every year sample multiple males in multiple courtships prior to choosing mates (Uy et al. 2001; Coleman et al. 2004). Since 1995, intensive color-marking of individuals in the population has resulted in all adult males and most females (91%) uniquely marked for identification in 2001, the year of this study. The use of automated video cameras at males' bowers (display sites) allows me to reconstruct complete female mate searching patterns (all courtships and copulations) for numerous individual females (Uy et al. 2000, 2001a, b; Coleman et al. 2004). Because females consistently return over multiple mating seasons (Uy et al. 2000, 2001a, b; Coleman et al. 2004), my sample of eighty-four females includes first-year females with no previous mating experience through females that have more than six years of mating experience. This range of female ages and levels of mating experience allows me to test hypotheses about the importance of female age and experience in mate choice.

Male satin bowerbirds have complex sexual displays comprised of multiple traits used by females in mate choice (Borgia 1985; Borgia & Loffredo 1986;

Patricelli et al. 2002; Coleman et al. 2004). Males build specialized stick structures, called bowers, where courtship and copulation occur (Borgia 1985), and they decorate the areas in front of their bowers with various objects collected from the environment (Marshall 1954; Borgia 1985; Hunter & Dwyer 1997); females prefer males with well-decorated bowers as mates (Borgia 1985; Coleman et al. 2004). When a female arrives at a bower for courtship, the male begins an elaborate behavioral display. This display is intense: during courtship, in close proximity to the female, the male puffs his feathers (ptiloerection), extends his wings, and runs across the bower platform while producing a loud mechanical buzzing vocalization (Loffredo & Borgia 1986; Patricelli et al. 2002). Females prefer the most intensely displaying males as mates, yet these intense displays frequently startle females (Patricelli et al. 2002, 2004). To ameliorate the threatening effects of intense displays, females signal the level of display intensity they will tolerate by 'crouching' – exaggerated movement downwards while tilting forwards (Patricelli et al. 2002, 2004). Successful males must adjust their display intensity in response to female crouching (Patricelli et al. 2002). Males that fail to appropriately adjust their display intensity startle females, which may result in termination of the courtship by the female (Patricelli et al. 2002, 2003). Typically, females sample multiple males in multiple courtships prior to choosing a single male as a mate (Uy et al. 2000; Coleman et al. 2004).

Hypotheses and predictions

Previous studies of satin bowerbirds show that females differ in their tolerance of intense male displays with age or experience as likely causes (Coleman et al. 2004; Patricelli et al. 2004). The hypothesis that intense displays are more threatening to young females than to old females leads to three testable predictions. First, as females gain tolerance for intense male displays, they should actively solicit higher-intensity displays from males. Thus, I predict an age-related increase in the degree of female crouching during courtship. Second, if older females crouch more than younger females, and thus signal they will tolerate higher intensity displays than will younger females, then I predict that male display intensity increases with female age. Third, I suggest that young females with little mating experience are highly threatened by intense male displays. Thus, I predict an age-related decrease in the frequency of female startling.

Female tolerance of intense male displays may also affect female mate searching effort: Patricelli et al. (2004) found a negative correlation between the frequency of female startling and the number of courtships a female initiated; they suggested that frequent startling disrupts a female's ability to assess males, and forces her to invest more in mate searching effort than if she was rarely startled. Patricelli et al.'s (2004) hypothesis that frequent startling increases female mate searching effort predicts a positive relationship between the frequency of female startling and (i) the number males sampled and (ii) the number of courtships initiated. The third prediction (above) suggests that female age affects female startling, thus I also predict

an age-related decrease in the number of males sampled and number of courtships initiated.

Empirical support for my predicted age-related differences would be consistent with the hypothesis that with age and experience females become more tolerant of, and less threatened by, intense male displays. This support alone would not identify the causes of the age-related differences. Recent studies of satin bowerbirds showed that female fidelity to their mates from the previous year affected female crouching and startling (Patricelli et al. 2003), and the number of males sampled and number of courtships initiated (Uy et al. 2000). Thus, age-related differences in these variables may be due to age-related differences in female fidelity; this predicts a positive relationship between female age and the likelihood females are faithful to their mates from the previous year.

METHODS

This study was conducted in 2001 on a natural population of satin bowerbirds at Wallaby Creek, New South Wales, Australia. From 1 September through 28 October, I captured birds using baited traps and mist nets. Each individual was fitted with three plastic leg bands arranged in a unique color combination, and one metal band displaying each individual's Australian Bird and Bat Banding Scheme number. Throughout the mating season (1 November – 20 December), 33 bowers were monitored using an automated video monitoring system. At each bower, an infrared

detector controlled a Sony Hi-8 camcorder via a custom designed control box powered by a 12-volt battery (Borgia 1995). A signal from the infrared detector to the control box turned on power to the camcorder for 40 s, and 40 s past the last time the detector was tripped if the camcorder was already running. Camcorders positioned at each bower were checked twice daily so that tapes could be changed before they ran out. All individuals observed in courtship were identified on video footage from their colored-band combinations. I classified an individual as 'female' only if she was observed copulating on video tape. This marking and monitoring system allowed me to reconstruct complete female mate searching patterns, and to quantify crouching and startling during courtship for 84 females: 10 first-year females, 8 second-year females, 9 third-year females, 17 fourth-year females, 17 fifth-year females, and 24 females that were at least six years old ('six-plus' [6+] females).

Females visit multiple males for multiple courtships prior to choosing mates (Uy et al. 2000, 2001a, b), and female startling and crouching, and male display intensity are affected by courtship order (Patricelli et al. 2003). Thus, for each female I quantified crouching, startling, and male display intensity in initial courtships only.

To quantify female crouching during courtship, I used a crouch index similar to Patricelli et al. (2003) that reflects crouch position. I divided the natural range of female motion into six positions which could be reliably scored, and I measured the maximum crouch achieved in each courtship. This measure differs from Patricelli et al.'s (2003) crouch index which also incorporated the time spent in each crouch position. For each female, I calculated the mean maximum crouch in initial courtships with all the males she sampled in 2001.

Startling was scored when a female that was inside the bower moved rapidly upward and/ or backward immediately (< 1 sec.) following a male's intense display (Patricelli et al. 2002, 2003). Consistent with Patricelli et al. (2002, 2003), I calculated the 'startle rate' as the proportion of intense displays that startled females. For each female, I calculated the mean startle rate during initial courtships with all the males she sampled in 2001. To determine the effect of female startling on mate searching effort (i.e. Patricelli et al. 2003), I used analysis of covariance (ANCOVA) to control for age-related differences in the number of males sampled and number of courtships initiated.

Also for each female, I calculated male display intensity in the initial courtships with each of the males sampled. Using the methods of Patricelli et al. (2002, 2003), I calculated display intensity based on three variables: (i) the distance run by the male during his display, (ii) the degree of male ptiloerection, and (iii) the location of the male on the bower platform. For each female, I calculated the mean male display intensity among all of the males she sampled.

To test the 'fidelity hypothesis', I compared crouching, startling, number of males sampled, and number of courtships initiated between females that in 2001 were faithful to their mates from 2000 and females that switched mates in 2001. I used logistic regression analysis to evaluate the relationship between female age and fidelity.

For all statistical tests, I used SAS and Statistica Version 6. Least-squares linear regression were used to investigate whether female age affected crouching, startling, male display intensity, number of males sampled, and number of courtships

initiated. I used ANOVA to investigate age affects among these same variables. If an ANOVA revealed significant age effects, then I used Student's *t*-tests to investigate differences among specific means (Sokal & Rohlf 1995). To determine the independent effects of startling on the number of males sampled and number of courtships initiated, I used ANCOVA to control for age effects on these variables. I used logistic regression analyses to investigate whether older females were more likely to be faithful to previous mates than were younger females. I used Student's *t*-tests to compare mean female crouching and startling, male display intensity, number of males sampled and number of courtships initiated between faithful and unfaithful females. All tests were two-tailed.

RESULTS

Effects of female age on female crouching, female startling, and male display intensity

Female age and crouching were positively related ($r^2 = 0.89$, $F_{1,4} = 33.57$, $P = 0.004$) (Figure 1a); males responded by increasing their display intensity as female age increased ($r^2 = 0.86$, $F_{1,4} = 25.44$, $P = 0.007$) (Figure 1b). The relationship between female age and startle rate was negative ($r^2 = 0.79$, $F_{1,4} = 15.20$, $P = 0.018$) (Figure 1c). These results support the hypothesis that older females are more tolerant of, and less threatened by, intense male displays than are younger females.

ANOVA revealed significant age effects in female crouching ($F_{5,78} = 12.19$, $P < 0.0001$), startling ($F_{5,78} = 9.43$, $P < 0.0001$), and male display intensity ($F_{5,78} = 10.68$, $P < 0.0001$). Pairwise comparisons of means revealed that second- and third-year females crouched more than first-year females but less than older females (Figure 1a). Males displayed less intensely to first-year females than to older females, and less intensely to second-year females than older females (Figure 1b), with the most intense displays to six-plus females (Figure 1b). First-year females startled more frequently than second- and third-year females, who startled more frequently than older females (Figure 1c).

Number of males sampled and number of courtships initiated

Female age explained a significant amount of the variation in the number of different males sampled ($r^2 = 0.74$, $F_{1,4} = 11.27$, $P = 0.02$; Figure 2a) and the total number of courtships initiated ($r^2 = 0.84$, $F_{1,4} = 21.24$, $P = 0.009$) (Figure 2b). Regression analyses showed that the rate of female startling affected the number of males sampled ($r^2 = 0.16$, $F_{1,82} = 15.00$, $P = 0.0002$) and the number of courtships initiated ($r^2 = 0.14$, $F_{1,82} = 14.47$, $P = 0.0003$). To control for age-effects, we used ANCOVA, and found that the frequency of female startling explained a significant amount of the variation in the total number of courtships initiated ($F_{5,77} = 4.47$, $P = 0.03$) and was marginally related to the number of different males sampled ($F_{5,77} = 2.77$, $P = 0.09$).

These results support the hypothesis that startling negatively affects female mate assessment (Patricelli et al. 2004).

ANOVA revealed significant female age effects in the mean number of males sampled ($F_{5,78} = 7.22$, $P = 0.001$) and mean number of courtships initiated ($F_{5,78} = 16.49$, $P < 0.0001$). Pairwise comparisons of means (Sokal & Rohlf 1995) revealed that prior to choosing mates, first- and second-year females sampled more males than did older females (Figure 2a), and that prior to choosing mates, first-, second-, and third-year females initiated more courtships than did older females (Figure 2b).

Tests of the fidelity hypothesis

If female fidelity to previous mates explained the age-related differences I observed, then I expected an age-related increase in the likelihood a female was faithful. While faithful females startled less ($t_{52} = -2.06$, $P = 0.04$), sampled fewer males ($t_{52} = -2.27$, $P = 0.03$), and initiated fewer courtships ($t_{52} = -2.05$, $P = 0.04$) than did females that switched mates (see also, Uy et al. 2000; Patricelli et al. 2003), logistic regression analysis showed that female age did not affect fidelity to previous mates ($\chi^2 = 0.22$, d.f. = 1, $P = 0.64$). And thus, female fidelity did not explain the age-related differences in female mate choice behaviors. While Patricelli et al. (2003) found that faithful females crouched more than females that switched mates, I did not find a difference in mean crouching between faithful and unfaithful females ($t_{52} = -1.61$, $P = 0.11$).

DISCUSSION

Identifying the causes of female preference variation may help generate predictions about evolutionary change in both preferences and in preferred traits (Widemo & Sæther 1999). Here I identify the causes of female preference variation in satin bowerbirds: my results indicate age-related differences in female tolerance of intense male displays explain why young and old females use different male display traits in mate choice (Coleman et al. 2004). My results also suggest that frequent startling by young females may be costly because it results in them investing more in mate searching effort than older females. These results, combined with Coleman's (2005) findings that old females choose higher quality males than those chosen by young females, suggest that female satin bowerbirds require experience observing intense male displays over several years to use intense male displays. Until then, females may not garner the full benefits of mate choice.

Supporting the hypothesis that with age and mating experience females become more tolerant of, and less threatened by, intense male displays, I found an age-related increase in female solicitation of intense displays by deeper crouching (Figure 1a), and that males responded by displaying more intensely to old than to young females (Figure 1b). I also found an age-related decrease in the frequency of female startling during these displays (Figure 1c). There was an age-related decrease in mate searching effort: with age, females sampled fewer males and initiated fewer

total courtships prior to choosing mates (Figure 2a, b, respectively). When I controlled for female age, I found that the frequency of female startling explained a significant amount of the variation in the number of courtships initiated. These results support Patricelli et al.'s (2004) hypothesis that startling disrupts female assessment of males, and forces females to expend more mate searching effort than if they had not been startled.

Consistent with the findings of previous studies of satin bowerbirds, I found that females that were faithful to their mates from the previous year startled less, sampled fewer males, and initiated fewer courtships than did females that switched mates (see, Uy et al. 2000; Patricelli et al. 2003). However, I did not find support for the hypothesis that female fidelity explained the age-related differences in these behaviors. Instead, the age-related differences I found suggest that there are experience-related changes in female tolerance of intense male displays. Female satin bowerbirds are long-lived (> 27 years, G. Borgia unpub. data), and in each year females typically sample multiple males in multiple courtships prior to choosing mates (Uy et al. 2001b; Coleman et al. 2004). I suggest that several years of experience observing intense male courtship displays may be necessary for females to learn to use intense male displays effectively in mate choice; until then females choose mates based on non-threatening display traits, such as bower decorations (e.g. Coleman et al. 2004). Experience-related differences in females' use of complex male displays may not be unique to satin bowerbirds.

Perhaps nowhere are differences in female mating experience greater than in populations of long-lived species, where each mating season, females sample multiple

males in multiple courtships prior to choosing mates; this describes many species with lek-like mating systems (Trail & Adams 1989; Petrie et al. 1991; Fiske & Kålås 1994; Rintamäki et al. 1995; Backwell & Passmore 1996; Gibson 1996; Uy et al. 2001). I show that relative to lifespan, females develop a tolerance for intense male displays relatively early: by year four, females solicit and receive high-intensity displays from males (Figure 1a, b, respectively) and are rarely startled by these displays compared to first-, second-, and third-year females (Figure 1c). These age-specific differences in female crouching and startling coincide with similarly timed differences between years two and four where female mate searching effort is reduced (Figure 2a, b). Overall, these results suggest that females may be under selection to increase their tolerance of intense male displays early in their lifetimes, perhaps because intense male displays are good indicators of male 'quality', such as condition or vigor (Borgia & Presgraves 1998; Maynard Smith & Harper 2003). Thus, being able to use display intensity in mate choice may allow females to choose the best males (e.g. Coleman 2005). Why then, are young females so threatened by intense displays – first-year females were startled by approximately 65% of the intense displays they observed in courtships (Figure 1c) – that they are unable to use intense male displays in mate choice (Coleman et al. 2004)? There are several reasons why this may be so.

First, because intense male courtship displays share elements with aggressive displays, young females may not be able to react appropriately to these displays in the context of courtship, and combined with the threat of forced copulation by the courting and/ or marauding males (Uy et al. 2000), young females may be especially

uneasy during courtship. Second, young females may be learning to use complex male displays in mate choice, just as their same-aged male counterparts are practicing and refining their abilities to produce complex sexual displays (Vellenga 1980; Collis & Borgia 1992, 1993; Maxwell et al. 2004). This would suggest that young females may benefit from increased courtship experience, because each courtship provides them with opportunities to learn to assess complex and threatening male displays. In this way, sampling many males in numerous courtships would be adaptive for young females, even if increased mate searching effort increased the likelihood of forced copulations (e.g. Uy et al. 2000). Third, because I do not know the extent to which young females are successful at building nests and producing young, I do not know the degree to which the age-related differences in mate searching behaviors are related to reproductive success. If young females are unable to build nests and/ or produce young, and therefore sample males primarily to learn to use complex male displays in mate choice, then I expect they would be less tolerant of threat during courtship than would an older female who is actively seeking the best male to sire her offspring.

In satin bowerbirds the criteria for mate choice changes as a function of female age (Coleman et al. 2004) and possibly experience (Coleman 2005), and until now the causes of these differences were unclear. Age- and experience-related preferences, however, are not unique to satin bowerbirds (see, Kodric-Brown & Nicoletto 2001). I suggest that females in many species may require substantial mating experience in order to use threatening or complex male displays in mate choice. In these species, as in satin bowerbirds and guppies (Kodric-Brown &

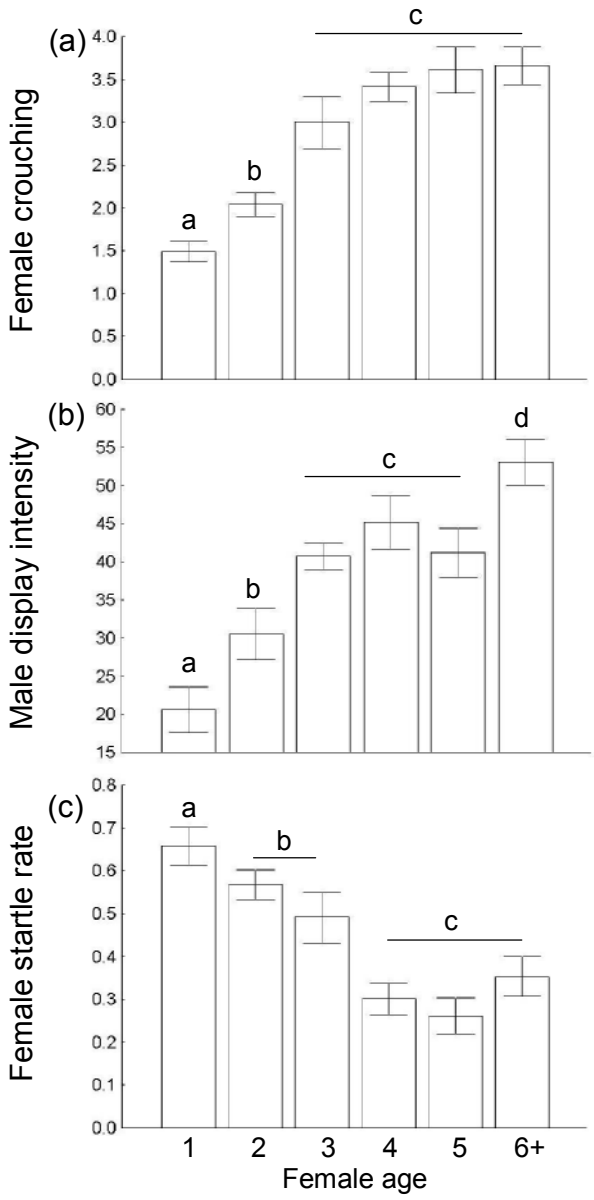
Nicoletto 2001; Coleman et al. 2004), young females with little mating experience may use only a subset of the male traits present during courtship, while old females with relatively extensive mating experience use a combination of display elements. By using multiple display traits in mate choice, experienced females may improve the accuracy of assessment or increase the amount of information they receive about a potential mate (i.e. Johnstone 1996; Møller & Pomiankowski 1993). Thus, experienced females may choose higher-quality males as mates (e.g. Coleman 2005).

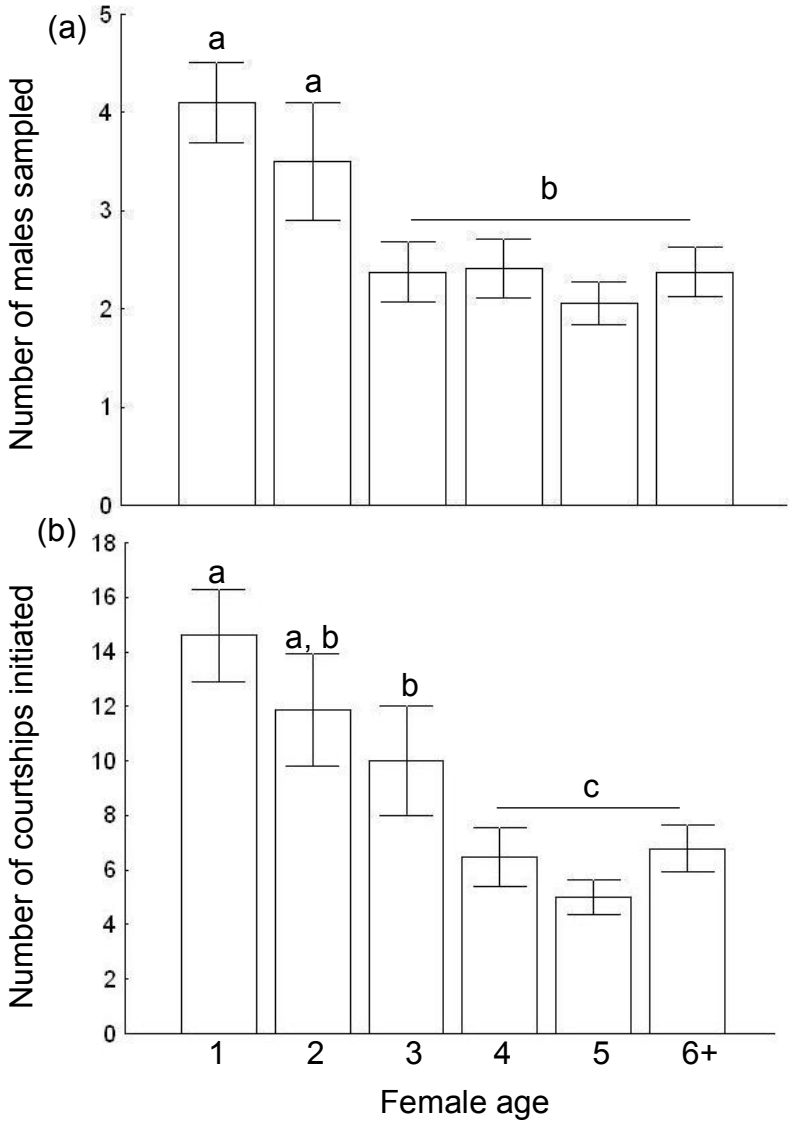
Males in many species have complex sexual displays comprised of multiple traits frequently produced across several sensory modalities (reviewed in, Hebets & Papaj 2005), and recent empirical work suggests that variable female preferences for particular male traits may help to explain the evolution of these complex displays (Brooks & Endler 2001; Kodric-Brown & Nicoletto 2001; Coleman et al. 2004). The striking similarity between age-specific use of particular male display traits by female guppies (Kodric-Brown & Nicoletto 2001) and satin bowerbirds (Coleman et al. 2004) suggests that I may be able to make predictions about what types of male traits may be associated with age- or experience-specific female preferences. Females may require substantial mating experience in order to use male displays that are multicomponent or that are threatening during courtship (Borgia 1995; Borgia & Presgraves 1998; Patricelli et al. 2002). Until sufficient experience is obtained, females may rely on a subset of relatively simple, single-component display traits in their mate choice decisions (see, Kodric-Brown & Nicoletto 2001; Coleman et al. 2004). I suggest that investigating the relationship between female experience, preference refinement, and the complexity of the male display traits used in mate

choice provides a promising direction for future empirical and theoretical studies of sexual selection.

Figure 1. The relationship between female age and mean (a) female crouching, (b) male display intensity, and (c) female startling. This figure shows an age-related increase in female solicitation of intense male displays (panel a), and that males responded by displaying more intensely to old females than to young females (panel b). First-, second-, and third-year females startled more frequently than older females (panel c). Bars and whiskers represent means ± SE. Bars with different letters above are significantly different ($P < 0.05$).

Figure 2. The relationship between female age and the mean (a) number of different males sampled in mate choice, and (b) total number of courtships initiated. This Figure indicates that females greatly improve in their mate assessment abilities within their first three years. Bars and whiskers represent means ± SE. Bars with different letters above are significantly different ($P < 0.05$).


(a)
Female crouching
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
a
b
c
(b)
Male display intensity
60
55
50
45
40
35
30
25
20
15
a
b
c
d
(c)
Female startle rate
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
a
b
c
1
2
3
4
5
6+
Female age


(a)
Number of males sampled
0
1
2
3
4
5
a
a
b
(b)
Number of courtships initiated
0
2
4
6
8
10
12
14
16
18
a
a, b
b
c
1
2
3
4
5
6+
Female age

CHAPTER III

Age-related improvement in female preferences suggests a learning component in mate choice

ABSTRACT

The ability to accurately discriminate among males is critical for females to choose high-quality mates. Here I test the hypothesis that the quality of males chosen as mates increases with female mating experience. In satin bowerbirds (*Ptilonorhynchus violaceus*), young females emphasize males' blue bower decorations in mate choice decisions, while old females emphasize male display intensity. I found that most females, regardless of age, preferred males with above-average numbers of blue decorations and above-average display intensity as mates, and that these 'above-average' males had fewer parasites than did other males. I also found that the parasite loads of preferred males decreased as a function of female age, suggesting that older females choose higher-quality mates than those chosen by younger females. Overall, these results suggest that young females are capable of discriminating among males using blue decorations, while the ability to more accurately discriminate among the top males using display intensity appears to be developed over time. The importance of experience for male display trait refinement is widely appreciated, yet the role

of mating experience in the improvement of female preferences has received little attention. Experience may be an important factor shaping female preferences in bowerbirds and other species in which females must discriminate among males with complex sexual displays.

INTRODUCTION

In many species males have elaborate sexual display traits that may indicate heritable aspects of male quality, such as condition (Kotiaho 2002; Saino et al. 2003; Scheuber et al. 2004; Hill et al. 2005), parasite resistance (Hamilton & Zuk 1982; Møller et al. 1999), or brain development (Nowicki et al. 2002; Buchannan et al. 2003; Spencer et al. 2003). Several sexual selection models predict that females prefer the males with the most extreme trait values as mates because display trait elaboration is proportional to male quality (Zahavi 1975; Hamilton & Zuk 1982). In many species with non-resource based mating systems there appear to be strong mating skews (Höglund & Alatalo 1995); often these skews reflect female preferences for males in central positions on leks, which supports the hypothesis that females prefer males with extreme displays. Even in resource-based mating systems where males provide resources that directly affect female fitness, there is evidence that females prefer extra-pair partners that have higher trait values than their social partners (Hamilton 1990; Westneat et al. 1990; Birkhead & Møller 1992; Møller 1998). This supports

that hypothesis that females use display trait elaboration to find extra-pair males of higher genetic quality than their social mates.

While there has been much interest and detailed information gathered regarding the development of male sexual displays – especially song (e.g. Catchpole & Slater 1995) – there is much less detailed information on how females develop the ability to choose their mates. Most sexual selection models have assumed that mate choice by females is a simple process, where females can easily discriminate among males that differ in display trait elaboration. Recent empirical studies, however, suggest that mate choice may be a much more complicated process. Females may develop specific preferences that change as a function of their age (Kodric-Brown & Nicoletto 2001; Moore & Moore 2001; Coleman et al. 2004), experience (Kodric-Brown & Nicoletto 2001), threat from predators (e.g. Breden & Stoner 1987), and social circumstances (Otter et al. 1998, 1999; Doutrelant & McGregor 2000). Moreover, mate searching can be a complex process where females sample multiple males in multiple courtships prior to choosing a single male as a mate (Moore & Moore 1994; Gibson & Langen 1996; Forsgren 1997; Uy et al. 2000, 2001a, b); recent empirical studies in distantly related taxa also show that a female's past mating experience may play an important role in her subsequent mate choice decisions (satin bowerbirds: Uy et al. 2000, 2001a, b; guppies: Kodric-Brown & Nicoletto 2001; wolf spiders: Hebets 2003).

In many species, males require time to learn and refine their sexual displays that are used to attract females in mate choice. Display trait learning may be particularly important in open-ended song learners (reviewed in, Beecher &

Brenowitz 2005), and in species with lek-like mating systems where males have complex multifaceted displays produced across several sensory modalities (satin bowerbirds: Vellenga 1970; Loffredo & Borgia 1986; Collis & Borgia 1992, 1993; Maxwell et al. 2004; Coleman 2005; long-tailed manakins: Trainer et al. 2002). Altogether, the complexity of female choice, evidence that females use past mating experience in subsequent mating decisions, and the requirement in many species that males must learn complex sexual displays suggests that there may be an important role for female experience in mate choice.

Coleman et al. (2004) showed that female satin bowerbirds have age-specific preferences for male displays, with young females preferring blue bower decorations – objects males use to decorate their display sites – and old females preferring male display intensity. They suggest that these differences may reflect young females' low tolerance for intense displays, but that once a female accumulates several years of mating experience she should switch to using male display intensity because display intensity is a better indicator of male quality than are blue decorations. According to this hypothesis, young females are using blue decorations because they are unable to use displays intensity in mate choice. This suggests that young females may be less able than old females to identify and choose the best males. I test this hypothesis by comparing the quality of the males chosen as mates by young and old females. If supported, this work would suggest that age- or experience-related differences in female preferences are critical in affecting the benefits of female choice, and would lead to important predictions about how females should allocate effort in the presence of differential mate choice costs and benefits.

Male satin bowerbirds have multifaceted sexual displays comprised of multiple traits used by females in mate choice. Males build specialized stick structures, called bowers, where courtship and copulation take place (Marshall 1954; Borgia 1985). They decorate the areas around their bowers with objects collected from the environment, and have strong preferences for blue objects (Borgia 1985). Males' courtship displays are intense and can threaten females, causing them to startle (Patricelli et al. 2002, 2003). In mate choice, the importance of intense displays versus bower decorations depends on female age (Coleman et al. 2004): young females emphasize blue decorations in mate choice decisions, while old females emphasize male display intensity. Under natural conditions, these two traits are correlated (Patricelli et al. 2003), thus young and old females should choose the same males as mates. To test this hypothesis, I investigate (i) the association between blue decorations and display intensity among males, (ii) whether young and old females choose the same males as mates, and (iii) the costs and benefits to females using male display intensity or bower decorations in mate choice.

To test whether females agree on which males are most attractive, I separated males into four groups based on the number of blue decorations and male display intensity: males with (i) below-average numbers of blue decorations and below-average display intensity, (ii) below-average numbers of blue decorations and above-average display intensity, (iii) above-average numbers of blue decorations and below-average display intensity, and (iv) above-average numbers of blue decorations and above-average display intensity. I predict that females of all ages prefer males with the most blue decorations and highest intensity displays as mates.

METHODS

This study was conducted in 2001 in a natural population of satin bowerbirds at Wallaby Creek, NSW, Australia. From 1 September through 28 October, I captured individuals using baited traps and mist nets. I fitted each individual with three plastic leg bands arranged in a unique color-combination. With males in-hand, I counted the number of lice nits around the eyes, and used the sum as my measure of parasite load for each male (Borgia et al. 2004). Nits of the louse, *Myrsidea ptilonorhynchi*, are the only abundant ectoparasite found on satin bowerbirds, and are only found regularly around the eye, where birds have difficulty preening (Borgia & Collis 1989, 1990).

From 1 November through 20 December, I monitored 33 bowers using an automated video monitoring system (Borgia 1995). I identified all individuals on video footage by their unique colored-band combinations. This marking and monitoring system allowed me to identify each female's mate. I followed 84 females throughout the mate searching process, and I separated these females into six age classes; intensive marking at Wallaby Creek since 1995 allowed me to age females up to six years. 'Six-plus' (6+) females were those females that in 2001 were at least six years old.

Intense male displays involve loud buzzing vocalizations, ptiloerection, and vigorous running across the bower platform with wings extended, all performed in close proximity to the female (Loffredo & Borgia 1986; Patricelli et al. 2002). For

each male, I calculated display intensity in the first courtship with each courted female. I calculated display intensity based on three variables: (i) the distance run by the male during his display, (ii) the degree of male ptiloerection, appearing larger, and (iii) the location of the male on the bower platform (Patricelli et al. 2002, 2003, 2004, in press).

I counted the numbers of blue decorations on males' bowers twice daily. For use in all analyses, I calculated the mean number of blue decorations for each male across the entire mating season.

To determine whether young and old females choose the same males as mates, I separated males based on numbers of blue decorations and display intensity. In the first analysis, I calculated the mean number of blue decorations and mean display intensity among all males in the population, and I determined whether young and old females chose males with similar trait values.

For all statistical analyses, I used SAS and Statistica (version 6). To investigate female discrimination, I separated males based on number of blue decorations and display intensity, and used Chi-square goodness-of-fit tests to evaluate whether females preferred particular males as mates. To determine the relationships between male parasite load and display intensity, and between male parasite load and numbers of blue decorations, I used Spearman's rank correlations (r_S). All tests are two-tailed unless otherwise noted.

RESULTS

Correlations between blue decorations and display intensity

I found that among all males in the population the number of blue decorations was strongly correlated with male display intensity ($r_S = 0.53$, $P = 0.002$). This association predicts that young and old females choose the same males as mates (i.e. Coleman et al. 2004).

Female preferences based on blue decorations and display intensity

To test for female preference agreement I separated males by mean trait values, creating four classes of males: males with below-average numbers of blue decorations and below-average display intensity (Figure 1, quadrant A), males with below-average numbers of blue decorations and above-average display intensity (Figure 1, quadrant B), males with above-average numbers of blue decorations and below-average display intensity (Figure 1, quadrant C), and males with above-average numbers of blue decorations and above-average display intensity (Figure 1, quadrant D). I found that most ($n = 59$; 70%) females regardless of age preferred males with above-average numbers of blue decorations and above average display intensity as

mates (Table 1). Thus, I investigated whether females discriminate among these 'above-average' males.

Benefits to females that use blue decorations versus display intensity in mate choice

I found that among all males in the population, numbers of ectoparasites were negatively correlated with blue decorations ($r_S = -0.50$, $P = 0.003$) (Figure 2a) and display intensity ($r_S = -0.64$, $P < 0.0001$) (Figure 2b), which suggests that these traits could inform females about male parasite load.

Among above-average males, however, there was no relationship between blue decorations and parasite load ($r_S = 0.13$, $P = 0.71$) (Figure 3a), while male display intensity was negatively correlated with parasite load ($r_S = -0.75$, $P = 0.01$) (Figure 3b); Because young females emphasize blue decorations in their mate choice decisions (Coleman et al. 2004), they may not be able to choose the most parasite-free males as mates. In contrast, because old females emphasize male display intensity in their mate choice decisions (Coleman et al. 2004), they may preferentially mate with the most parasite-free males. I tested this hypothesis and found that the relationship between female age and the parasite load of males chosen as mates was strongly negative ($r_S = -0.94$, $P = 0.005$) (Figure 4).

DISCUSSION

In many species females prefer males with highly-exaggerated display traits as mates because the degree of display trait exaggeration is assumed to be proportional to some heritable aspect of male quality (Borgia 1979; Hamilton & Zuk 1982; Andersson 1994; Candolin 2003). Thus, females that prefer the males with the most highly exaggerated traits as mates, benefit by choosing high-quality males as mates (reviewed in, Andersson 1994). This hypothesis predicts that within populations, females prefer the same males as mates, yet this is seldom the case (Mackenzie et al. 1995; Kokko & Lundström 1997). While there are several hypotheses to explain disagreement among females in mate choice (such as inbreeding avoidance, genotype matching, and female-female competition, among others [reviewed in, Jennions & Petrie 1997; Widemo & Sæther 1999]), the hypothesis that variable female preferences may reflect differences in the females' abilities to discriminate among potential mates has not been tested. Here I tested this hypothesis, and found that (i) there are differences in the informative value of particular male display traits depending on which males a female samples, and (ii) that age-specific use of particular male display traits affects results in older females being better than younger females at identifying and choosing high-quality males as mates.

I found a positive correlation between blue decorations and male display intensity (Figure 1). Based on this relationship, I predicted that young and old females would choose the same males as mates (e.g. Coleman et al. 2004). Indeed, most females (n = 59; 70%), regardless of age, preferred males with above-average

numbers of blue decorations and above-average display intensity (Figure 1, Table 1). These results show that females of all ages prefer males with above-average traits values as mates.

I then investigated whether age-specific female preferences for blue decorations versus display intensity (i.e. Coleman et al. 2004) resulted in differences in the benefits of mate choice. Among all males, the numbers of blue decorations and male display intensity were both negatively correlated with male parasite load (Figure 2). Thus, by choosing males based on numbers of blue decorations and/ or display intensity females may benefit by choosing parasite free males as mates. Among the subset of males with above-average numbers of blue decorations and display intensity, I found that while display intensity was negatively correlated with male parasite load (Figure 3b), there was no relationship between blue decorations and parasite load (Figure 3a). These results suggest that among above-average males, display intensity but not blue decorations may inform females about male parasite resistance. Thus, old females that emphasize male display intensity in mate choice decisions (Coleman et al. 2004) may choose relatively parasite-free males compared to males chosen by young females who emphasize blue decorations in mate choice decisions (Coleman et al. 2004). I tested this hypothesis and found that the parasite loads of preferred males decreased as a function of female age (Figure 4), suggesting that age-related differences in the display traits used in mate choice results in age-related differences in females' abilities to discriminate among males and in differences in the quality of males chosen as mates.

Understanding what information male displays traits provide females in mate choice has been a central focus in studies of male display trait evolution (reviewed in, Andersson 1994; Candolin 2003). Models of multiple display trait evolution suggest that multiple traits (i) provide information to females about different aspects of male quality ('multiple messages': Møller & Pomiankowski 1993; Johnstone 1996), (ii) allow for more accurate assessment of male quality as each trait reflects the same aspect of male quality ('redundant signals': Møller & Pomiankowski 1993; 'backup signals': Jonhstone 1996), or (iii) do not indicate male quality, but instead take advantage of arbitrary female preferences ('unreliable signals': Møller & Pomiankowski 1993). According to these definitions, among all males in the population, blue decorations and display intensity may function as redundant signals, both informing females of male quality and possibly of parasite resistance. Among the preferred males with above-average displays, however, blue decorations do not inform females about male quality, while display intensity continues to inform. Thus, among above-average males, blue decorations and display intensity are not redundant signals. These finding suggest that whether multiple male display traits function as redundant signals may depend on which males are sampled. This is the first study to show that the information that male display traits provide to females in mate choice can depend on which males a female samples.

I show that age-specific use of male display traits results in differential benefits of mate choice. Young females, whose mate choice decisions emphasize blue decorations (Coleman et al. 2004), chose males with higher parasite loads than males chosen by older females. In contrast, older females, whose mate choice decisions

emphasize male display intensity (Coleman et al. 2004), chose males with fewer parasites than the males chosen by young females. I suggest that age- or experience-related differences in females' abilities to discriminate among males are not unique to satin bowerbirds. Males in many species have complex displays comprised of multiple exaggerated displays traits (reviewed in, Candolin 2003), and in some species these displays are refined over long periods of time before they are used to attract females in mate choice (Vellenga 1970; Loffredo & Borgia 1986; Collis & Borgia 1992, 1993; Trainer et al. 2002; Maxwell et al. 2004; Coleman 2005). I suggest that females in these species may develop their preferences through mating experience over similarly long periods of time. Until female preferences are fully developed, females may rely on only a subset of the traits available for assessment (see, Kodric-Brown & Nicoletto 2001; Coleman et al. 2004) and may not receive the full benefits of mate choice.

Table 1 Female preferences for males in different quadrants (see Figure 1). These results show that female of all ages preferred males with above-average numbers of blue decorations and above-average display intensity (Figure 1, quadrant B) as mates.

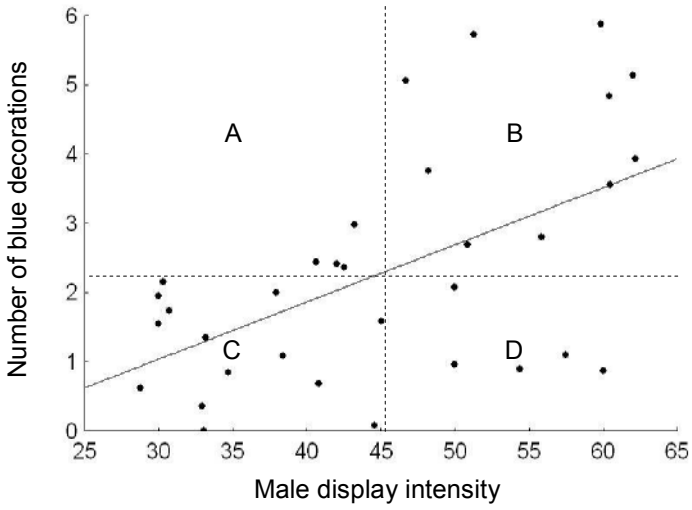
	Quadrant						
Female age	**A**	**B**	**C**	**D**	χ^2	**df**	***P***
First-year	1	7	0	2	9.73	3	0.02
Second-year	0	7	1	0	12.63	3	0.006
Third-year	1	6	0	1	8.80	3	0.03
Fourth-year	2	10	3	2	7.22	3	0.05
Fifth-year	2	12	1	2	14.74	3	0.002
Six-plus	0	17	1	6	26.00	3	< 0.0001
Total	6	59	6	13	71.30	3	< 0.00001

Figure 1. The relationship between blue decorations and male display intensity. I separated males into four quadrants (A, B, C, D) based on relative trait values (broad dashed lines represent mean trait values) and evaluated female preferences for males in each quadrant (see Table 1).

Figure 2. Among all males in my population: the relationship between male parasite load and (a) mean number of blue decorations, and (b) mean display intensity. This figure suggests that blue decorations and display intensity may inform females about male quality.

Figure 3. Among males with above-average numbers of blue decorations and above average display intensity: the relationship between male parasite load and (a) mean number of blue decorations, and (b) mean display intensity. This figure suggests that display intensity may inform females about the quality of above-average males, but that blue decorations may not.

Figure 4. The relationship between female age and the mean parasite load of males chosen as mates. This figure shows that with age, females choose males with fewer parasites.


Number of blue decorations
Male display intensity
A
B
C
D
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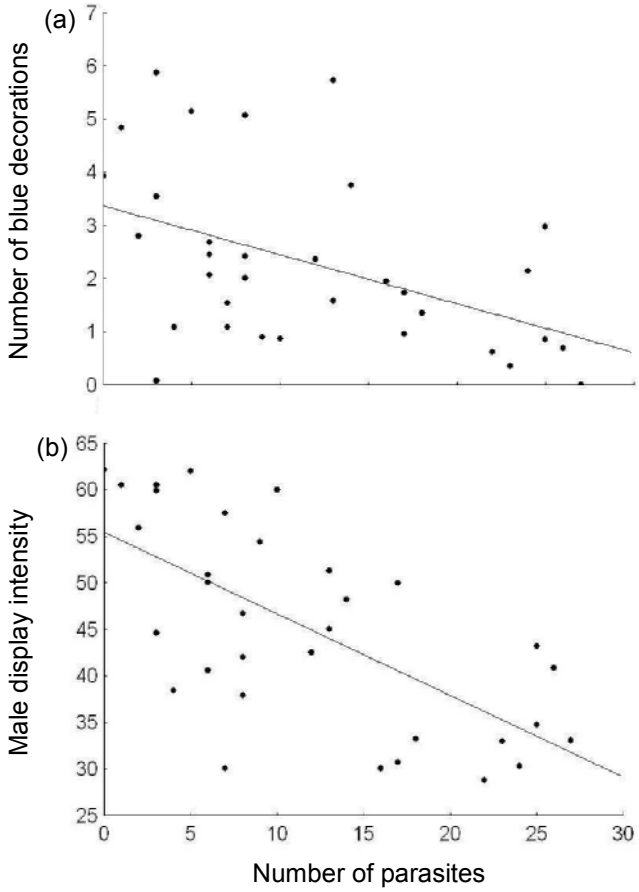
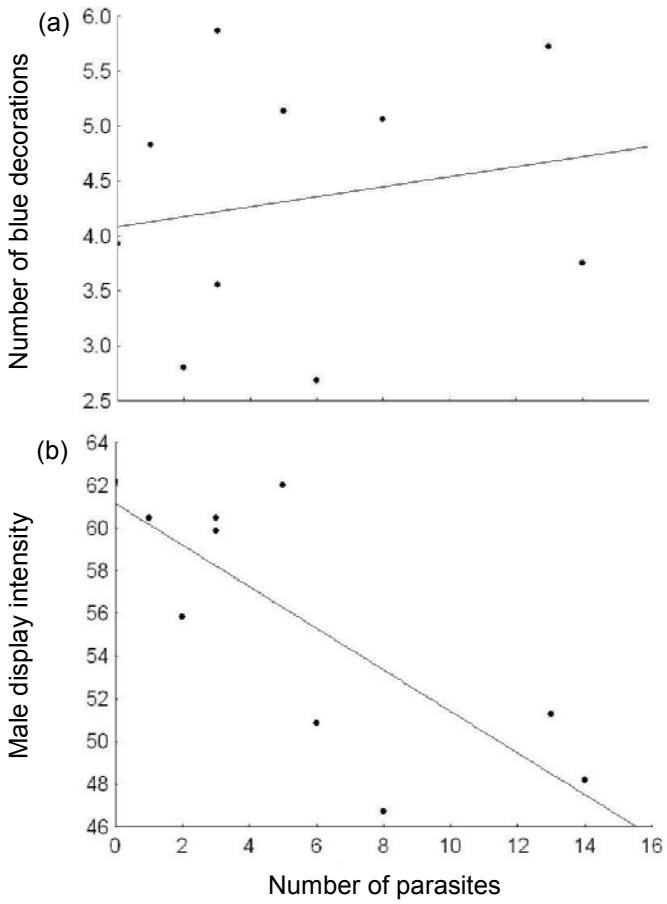
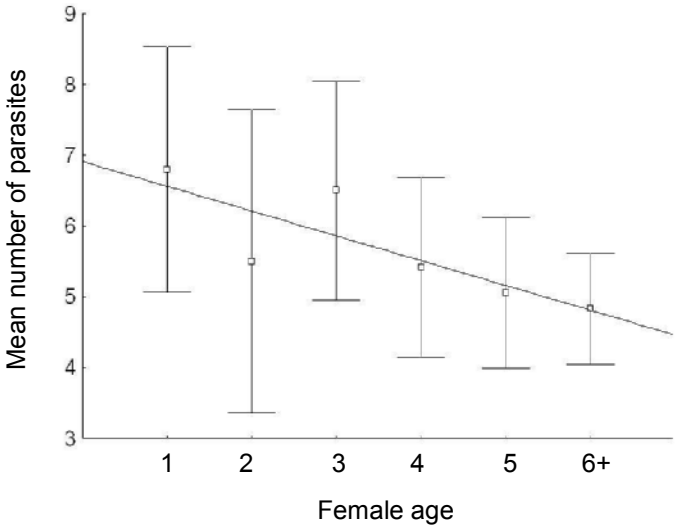
1
2
3
4
5
6
25
30
35
40
45
50
55
60
65


(a)
Number of blue decorations
0
1
2
3
4
5
6
7
(b)
Male display intensity
25
30
35
40
45
50
55
60
65
0
5
10
15
20
25
30
Number of parasites


(a)
Number of blue decorations
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
(b)
Male display intensity
64
62
60
58
56
54
52
50
48
46
0
2
4
6
8
10
12
14
16
Number of parasites


Mean number of parasites
9
8
7
6
5
4
3
1
2
3
4
5
6+
Female age

CHAPTER IV

Multiple display trait evolution: co-occurrence of threat-reducing traits and intense male displays affects female mate assessment and male attractiveness

ABSTRACT

Interactions among multiple male display traits may be important in female mate choice, but have received little attention. Males in many species have evolved intense behavioral displays that can threaten females during courtship. Thus, selection may favor the co-occurrence of threat-reducing display traits that calm females, which may facilitate mate assessment. I tested this hypothesis in satin bowerbirds, a species where males have complex sexual displays that combine intense behavioral displays that can cause females to startle during courtship, with non-threatening display elements such as bower decorations. In an experiment where I augmented males' blue bower decorations, I found that (i) females startled less frequently in courtships with males with augmented decorations ('experimental males') than in courtships with males with unaugmented decorations ('control males') – the calming effect of blue decorations was especially important in courtships with young females, (ii) females of all ages remained longer in courtships with experimental males than in courtships with control males, and (iii) experimental males were more

attractive than control males to first- and second-year females, but not to older females. These results support the hypothesis that bower decorations reduce the threat of intense male displays, especially to young females, and facilitate female mate assessment. Selection for threat-reducing traits that co-occur with males' intense courtship displays may help to explain the widespread occurrence of multifaceted male displays.

INTRODUCTION

In many species females use multiple male display traits in mate choice (reviewed in, Candolin 2003), and the evolution of multifaceted male displays is a controversial issue in behavioral and evolutionary biology (reviewed in, Andersson 1994). Models of multiple display trait evolution (Møller & Pomiankowski 1993; Johnstone 1996) and most empirical studies of multiple display traits typically focus on the function of individual traits and preferences (for exceptions see, Hasson 1989; Borgia 1995a; Rowe 1999; Hebets & Uetz 2000; Kodric-Brown & Nicoletto 2001; Patricelli et al. 2003; Hebets 2004). Recent work, however, suggests that in species where males have multifaceted sexual displays, interactions among multiple display traits may be common and affect female preferences; thus 'inter-signal interactions' (Candolin 2003; Hebets & Papaj 2005) may have important implications for the evolution of preferences and preferred traits. In the wolf spider, *Schizocosa uetzi,* for example, male courtship vibration functions as an attention-focusing trait that affects female

visual attention on male leg ornamentation (Hebets 2004); in the absence of courtship vibration, females are indifferent to leg ornamentation (Hebets & Uetz 2000). Thus, the interaction between these traits is critical for females to discriminate among potential mates.

Here I explore display trait interactions in a species where males have intense behavioral displays that can threaten females during courtship combined with non-threatening display traits that may ameliorate the threat of intense displays. Intense male displays are found across taxa (Borgia 1979; Loffredo & Borgia 1986; Berglund et al. 1996; Borgia & Presgraves 1998; Mateos & Carranza 1999; Borgia & Coleman 2001; Patricelli et al. 2002; Patricelli et al. 2003). In many species females prefer males with the most intense displays as mates (Ryan & Rand 1990; Zuk et al. 1995; Searcy 1996; Borgia 1998; Candolin & Reynolds 2001; Kodric-Brown & Nicoletto 2001; Parri et al. 2002; Patricelli et al. 2002; Sacchi et al. 2003), perhaps because intense displays are good indicators of male quality (Maynard-Smith & Harper 2003). However, intense male displays frequently share elements with aggressive displays (Borgia 1979; Berglund et al. 1996; Borgia & Coleman 2000) and can threaten females during courtship. Thus, selection should favor the evolution threat-reducing display traits in association with threatening display traits. To date, there have been only two tests of this hypothesis (Borgia & Pregraves 1998; Patricelli et al. 2002). Male spotted bowerbirds (*Chlamydera maculata*) have intense multimodal displays that they produce during courtship, and in some populations females observe these displays through the walls of a highly derived form of the male's bower (Borgia 1995a). Borgia and Presgraves (1998) showed that experimental removal of one wall

of the bower resulted in a reduction in male display intensity, and that males oriented themselves so that the remaining wall stood between them and the females during courtship. Also, males reduced their display intensity when females were not protected by the bower wall. Thus, the bower serves as a threat-reducing structure that allows females to observe intense behavioral displays in relative security (Borgia 1995a; Borgia & Presgraves 1998; Borgia & Coleman 2000). In satin bowerbirds (*Ptilonorhynchus violaceus*) males do not court females through bower walls, but instead modulate the intensity of their courtship displays in response to female signals that indicate the level of display intensity a female will tolerate (Patricelli et al. 2002, 2004). During courtship, successful males must adjust their display intensity appropriately to avoid startling females. Thus, sexual selection has driven the evolution of a communication system that allows males to match their display intensity to female tolerance for intense displays.

In addition to this threat-reducing communication system, recent work suggests that bower decorations – objects males use to decorate their bowers (Marshall 1954; Borgia 1985) – may also affect the threat of intense male displays in satin bowerbirds. Patricelli et al. (2004) found a negative correlation between the number of a male's bower decorations and the frequency that females startled during intense male displays. Thus, they proposed that the presence of blue decorations may calm females during intense displays, and thereby facilitate female mate assessment. I test this hypothesis directly by augmenting male satin bowerbirds' blue bower decorations, and evaluating the effects on female mate choice behaviors and other male display traits.

Male satin bowerbirds have multiple exaggerated display traits that are used by females in mate choice. Males build bowers, and they decorate their bowers with objects collected from the environment; males prefer to decorate with blue objects (Borgia et al. 1987), and females prefer males with many blue decorations as mates (Borgia 1985; Coleman et al. 2004). Males' courtship displays are intense and multimodal, coordinating ptiloerection, wing-extension, and running with a loud mechanical buzzing vocalization. While females prefer the most intensely-displaying males as mates, intense displays can threaten females, causing them to startle (Patricelli et al. 2004). To ameliorate the threat of intense male displays during courtship, females signal the level of display intensity they will tolerate by 'crouching' – exaggerated movement forwards and downwards (Patricelli et al. 2004). Successful males must observe female crouching and modulate their display intensity accordingly (Patricelli et al. 2002).

In satin bowerbirds, female tolerance of intense male displays depends on female age and experience in mate choice. Coleman et al. (2004) showed that first- and second-year females emphasized blue bower decorations in mate choice decisions, while older females emphasized male display intensity. These age-specific preferences are the result of young females being highly threatened by intense male displays compared to older, more experienced females (Coleman 2005). Coleman's (2005) hypothesis that young females are more threatened by intense male displays than are old females predicts that the calming effect of blue decorations may be especially important for young females. Thus, in this study I separate females by age,

and evaluate age-specific effects of the decoration augmentation experiment on female mate choice behaviors.

The hypothesis that bower decorations calm females during intense male displays which facilitates mate assessment (Patricelli et al. 2004) predicts that when I augment the number of bower decorations at males' bowers that (i) females crouch more and startle less in courtships with males with augmented decorations ('experimental males') than in courtships with males whose decorations are not augmented ('control males'), (ii) experimental males display more intensely than control males because female crouching signals the level of display intensity a female will tolerate, (iii) because they are less threatened by males with many blue decorations, females remain engaged in courtships longer with experimental males than with control males, and (iv) females prefer experimental males as mates. In each of the tests of these predictions, I separate females by age. Because young females are more threatened by, and less tolerant of, intense male displays than are old females (Coleman 2005), I predict that the augmentation of males' blue decorations will have the strongest effect on young females' mate choice behaviors.

METHODS

This work was conducted in 2000 at Wallaby Creek, New South Wales, Australia. Prior to the mating season, birds were captured using traps and mist nets. Each individual was fitted with three plastic leg bands arranged in a unique color-

combination. In my study population, all adult males and most (91%) of the females were uniquely marked for identification. From 1 November to 20 December, automatic Hi-8 video cameras recorded behaviors at 28 adjacent bowers. This monitoring provided a complete record of all courtships and copulations. Individuals were classified as female only if they were observed copulating with a male on videotape. Detailed mate sampling patterns and mate choice for 64 females were reconstructed from video footage.

Using information from 1998 (Uy et al. 2001), bower-owning males were paired to maximize similarity in mating success (number of different mates). The bower of one male in each dyad was randomly selected for augmentation with blue bower decorations ('experimental males'), while the other male's decorations remained unaugmented ('control males'). Twenty blue tiles (2.54 cm x 2.54 cm) and 50 strands of blue plastic (25cm x ~0.20cm) were placed in caches 1 meter from the bower platform. Within 2 hours, each experimental male placed all of the tiles and plastic strands on his bower platform. Blue plastic strands are frequently used as bower decorations in the Wallaby Creek population, and the number of strands used in the augmentation was within the range of plastic strands displayed by bower owing males prior to the augmentation (mean number ± s.e. of plastic strands on bowers prior to the experiment: 45 ± 7.73) (S. W. Coleman, G. Borgia, in prep.). To prevent decoration stealing (Borgia & Gore 1986), after experimental males placed their tiles, each tile was glued to the head of a long screw then secured into the ground. Plastic strands were frequently woven into the bower platform by bower owners, likely reducing the frequency of stealing (S. W. Coleman, G. Borgia, pers. obs.). Twice a

day at each bower, the numbers of tiles and plastic strands were counted and replaced to original levels if necessary. Tiles and plastic strands found on the bowers of control males as a result of decoration stealing were removed. All other bower decorations (Borgia 1985) remained unmanipulated.

I grouped females based on their years of mating experience. 'Three-plus' females had at least 2 years of prior mating experience. 'Second-year' females had 1 year of prior mating experience. 'First-year' females were not previously observed mating. All first-year females (n = 16) were captured and marked for the first time in those years. All females used in my analyses were courted by at least one experimental male and one control male.

Startling was scored when a female that was inside the bower moved rapidly upward and/ or backward immediately (< 1 sec.) following a male's intense display (Patricelli et al. 2002, 2003). Consistent with Patricelli et al. (2002, 2003), I calculated the 'startle rate' as the proportion of intense displays that startled females. For each female, I calculated the mean startle rate during first courtships with all the males she sampled, and compared age-specific female startle rates in courtships with control versus experimental males.

To quantify female crouching during courtship, I divided the natural range of female motion into six positions which could be reliably scored (see also, Patricelli et al. 2003, 2004), and I measured the maximum crouch achieved in each courtship. For each female, I calculated the mean maximum crouch in first courtships with all the males sampled, and compared age-specific female crouching in courtships with experimental versus control males.

Intense male displays involve loud buzzing vocalizations, ptiloerection, and vigorous running across the bower platform with wings extended, all performed in close proximity to the female (Loffredo & Borgia 1986; Patricelli et al. 2002). For each male, I calculated display intensity in the first courtship with each courted female. I calculated display intensity based on three variables: (i) the distance run by the male during his display, (ii) the degree of male ptiloerection, appearing larger, and (iii) the location of the male on the bower platform (Patricelli et al. 2002, 2003, 2004, in press).

I used SAS and Statistica version 6 for all statistical analyses. For use in statistical analyses, I calculated mean female crouching and startling, courtship duration, and male display intensity in courtships with experimental and control males. Preliminary analyses showed no pairwise differences in these variables between first- and second-year females, so I combined first- and second-year females into a single group for pairwise mean comparisons. All tests are two-tailed.

RESULTS

There were no differences in female crouching behavior or male display intensity in courtships with experimental males versus control males (Table 1). However, I found support for the hypothesis that blue bower decorations calm females during intense male displays: first- and second-year females startled less frequently in courtships with experimental males than in courtships with control males (Figure 1a), and three-

plus females tended to startle less frequently in courtships with experimental males than in courtships with control males (Figure 1b). I also found for females of all ages that courtship duration was greater in courtships with experimental males than in courtships with control males (Figure 2), and that the frequency of female startling explained a significant amount of the variation in courtship duration ($r^2 = 0.16$, $F_{1,24} = 4.77$, $P = 0.03$).

I predicted that if the augmentation of blue decorations reduced the threat of males' intense displays, then experimental males would be more attractive to females as mates. Overall, there was no difference between experimental males' mean mating success (2.71 ± 0.46) and control males' mean mating success (1.93 ± 0.51) ($t_{26} = 1.14$, $P = 0.26$). However, when I partitioned male mating success by female age class, I found that the decoration augmentation experiment had a significant effect on male mating success with first- and second-year females but did not affect male mating success with three-plus females (Table 1).

DISCUSSION

Interactions among multiple male displays traits may be important in female mate choice, and may help explain the evolution of complex male displays (reviewed in, Hebets & Papaj 2005). My results support the hypothesis that one function of male satin bowerbirds' blue bower decorations is to calm females, especially young females, during intense male displays, and that this calming effect facilitated female

mate assessment. I show that first- and second-year females startled less in courtships with males whose blue decorations were augmented (experimental males) than in courtships with males whose blue decorations were not augmented (control males) (Figure 1); older females tended to startle less in courtships with experimental males than in courtships with control males (Figure 1), though the difference was non-significant ($P = 0.09$). Differences in the frequency of female startling were not explained by differences in male display intensity between experimental and control males (Table 1).

Patricelli et al. (2004) showed that frequent female starling increased female mate searching effort – which is costly to females (see, Uy et al. 2000). Thus, I predicted that if the presence of blue decorations calms females (i.e. Figure 1), then the presence of blue decorations may also affect female mate assessment behavior. Supporting this hypothesis, I found that females of all ages remained engaged in courtship longer with experimental males than with control males (Figure 2), and that a significant amount of the variation in courtship duration was explained by the frequency of female startling. Blue decorations appear to affect courtship duration through their direct effect on female startling. This hypothesis could be tested in an experiment where blue decorations are removed from the bower. The prediction would be that females startle more frequently at bowers where decorations are removed.

Augmenting blue decorations increased the attractiveness of males to first- and second-year females, but not to older females (Table 1). These results are consistent with Coleman et al.'s (2004) findings that young females emphasize blue

decorations in mate choice decisions while old females emphasize male display intensity. It is important to note that overall, there was no difference between experimental and control male mating success. Thus, had I not separated females by age and evaluated male mating success, I may have concluded that the decoration augmentation experiment had no effect on female preferences and male mating success. Future studies of mate choice that investigate female preferences for particular male display traits may be careful not to assume that all females respond alike to display trait manipulations.

Overall, my results support the hypothesis that sexual selection drives the evolution of threat-reducing display traits that co-occur with threatening display traits. To date, all empirical tests of this hypothesis come from bowerbirds (Borgia & Presgraves 1998; Borgia & Coleman 2000; Patricelli et al. 2002, 2004), which is surprising given how widespread intense, potentially-threatening male displays are among taxa (Borgia 1979; Andersson 1994; Berglund et al. 1996; Borgia & Coleman 2000) and that females in many species prefer the most intensely-displaying males as mates (Ryan & Rand 1990; Zuk et al. 1995; Searcy 1996; Borgia 1998; Candolin & Reynolds 2001; Kodric-Brown & Nicoletto 2001; Parri et al. 2002; Patricelli et al. 2002; Sacchi et al. 2003). Intense male displays are commonly used by females in mate choice, perhaps because they are good indicators of male 'quality', such as parasite resistance or vigor (Hamiton & Zuk 1982; Borgia & Presgraves 1998; Maynard Smith & Harper 2003). However, intense displays frequently share elements with aggressive displays (e.g. Borgia 1979; Loffredo & Borgia 1986; Berglund et al. 1996; Borgia & Presgraves 1998; Mateos & Carranza 1999; Borgia & Coleman 2001;

Patricelli et al. 2002; Patricelli et al. 2003) and can threaten females during courtship. Thus, sexual selection should favor the evolution of male display traits that reduce the threat of intense displays; there has been only one explicit test of this hypothesis. Borgia and Presgraves (1998) showed in spotted bowerbirds (*Chlamydera maculata*) that experimental removal of one bower wall resulted in males courting exclusively on the side of the bower with the remaining wall, keeping the wall between themselves and courted females; males that courted through the remaining wall displayed more intensely than males displaying behind the destroyed wall. Here I show that bower decorations can also function in threat reduction (see also, Patricelli et al. 2004), but with one important difference: blue decorations do not form a physical barrier between females and males during courtship. So why do blue decorations calm females during intense male displays?

During courtship, female satin bowerbirds must remain vigilant against forced copulation attempts from courting males and from marauding males that disrupt courtship (Borgia 1995b; Uy et al. 2001). Perhaps females use the presence of blue decorations as a measure of the costs of forced copulation with the bower owning male. Intrasexual competition for blue decorations is intense with rival males frequently stealing each others' decorations (Borgia & Gore 1986), and because blue objects are rare in the environment (Borgia et al. 1987), females may use the number of blue decorations as an indication of male dominance or condition (Borgia et al. 1985; Borgia & Gore 1986); Coleman (2005) also showed that blue decorations may indicate male parasite load. Females may therefore reduce their vigilance against forced-copulation from bower owners when the owners have many blue decorations

because the costs of forced copulation are less with a male with a well-decorated bower than with a male with a poorly-decorated bower. The ability to reduce vigilance – and startling – may be adaptive because it facilitates mate assessment and because it may also reduce the costs of mate searching (Uy et al. 2001; Patricelli et al. 2004; Coleman 2005). Alternatively, males may preferentially decorate their bowers with blue objects (Borgia et al. 1987) to exploit the startle-inhibiting effects of blue decorations on females. This hypothesis suggests that the color blue inhibits startle behavior, and that males evolve displays to exploit this sensory bias (e.g. Ryan 1990). Research in rats and humans has shown that the startle response may be inhibited by 'pleasant' stimuli (Lang 1995; Koch 1999); blue decorations may have a similar effect. This hypothesis seems unlikely, however, because it suggests that startling, even though potentially costly, can persist for no reason only to be abated by uninformative blue decorations.

Males in many species have complex sexual displays comprised of multiple signals produced across multiple sensory modalities (Andersson 1994; Candolin 2003; Hebets & Papaj 2005), yet few studies have investigated how interactions among multiple traits affect female mate choice decisions, and how trait interactions affect display trait evolution (for exceptions see, spotted bowerbirds: Borgia & Presgraves 1998; wolf spiders: Hebets & Uetz 1999, Hebets 2004; satin bowerbirds: Patricelli et al. 2004). I show that the expression of a non-threatening visual display trait reduces the threat of intense multimodal male displays, especially to young females, and facilitates female mate assessment. Because intense male displays are widespread, I suggest that threat-reducing traits may be similarly common (see also,

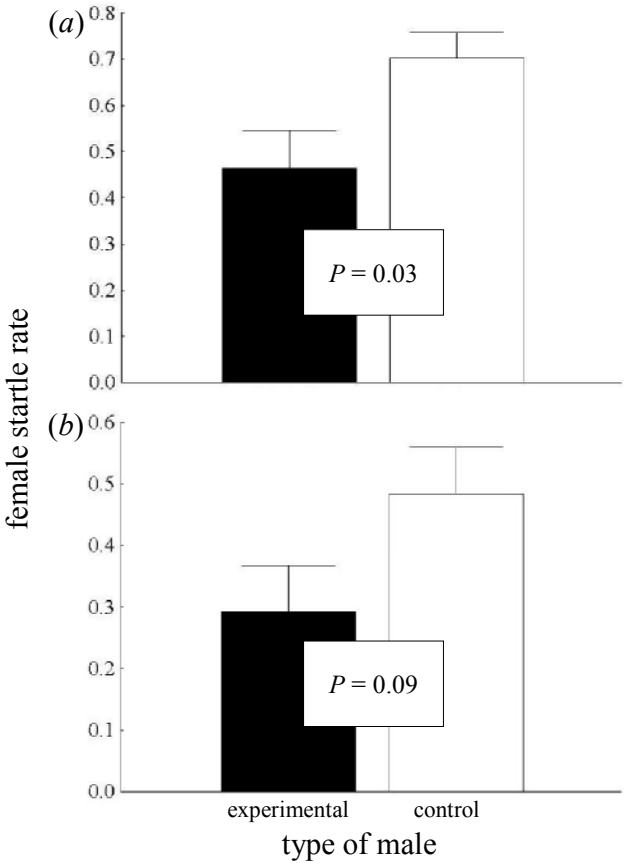
Borgia 1995a). If so, then the co-occurrence of threatening and threat-reducing traits may help to explain the function and evolution of many multifaceted male displays.

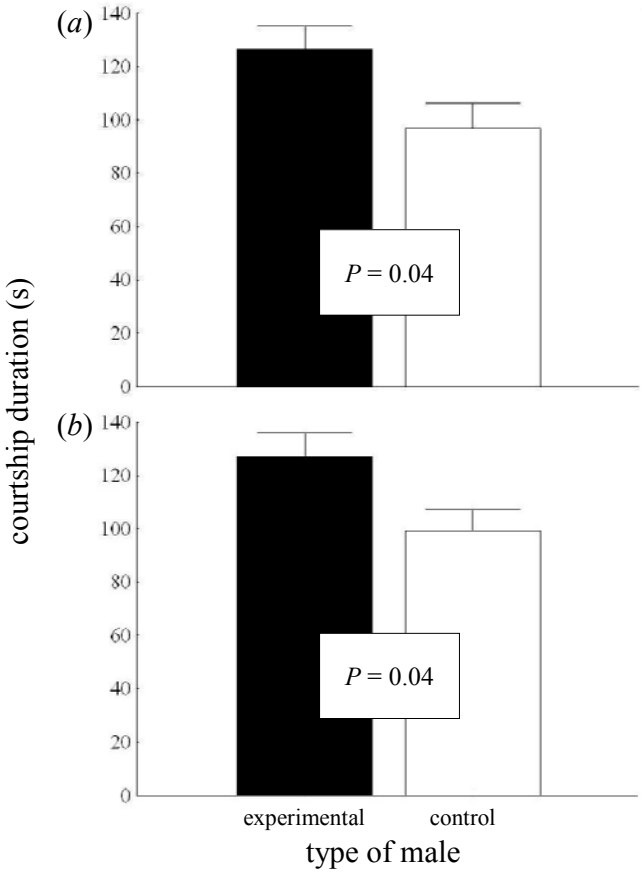
Table 1 Pairwise comparisons of female crouching, male display intensity, and male mating success (ms) in courtships with experimental and control males

variable	female age	experimental male mean ± se	control male mean ± se	*t*	df	*P*
crouching	$1^{st}/2^{nd}$ year	1.97 ± 0.13	1.73 ± 0.11	1.39	9	0.20
crouching	three-plus	2.23 ± 0.08	2.18 ± 0.06	0.57	15	0.56
intensity	$1^{st}/2^{nd}$ year	30.46 ± 0.94	29.46 ± 0.72	0.86	9	0.41
intensity	three-plus	36.38 ± 2.43	35.77 ± 2.08	0.28	15	0.78
ms	$1^{st}/2^{nd}$ year	1.71 ± 0.33	0.28 ± 0.16	3.80	26	0.008
ms	three-plus	1.00 ± 0.23	1.57 ± 0.38	-1.26	26	0.22

Figure 1. The effect of the decoration augmentation experiment on the startle rates of (*a*) first- and second-year females and (*b*) three-plus females in courtships with experimental and control males.

Figure 2. The effect of the decoration augmentation experiment on courtship duration in courtships with (*a*) first- and second-year females' and (*b*) three-plus females.


(a)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
P = 0.03
(b)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
P = 0.09
female startle rate
experimental
control
type of male


(a)
(b)
140
120
100
80
60
40
20
0
P = 0.04
P = 0.04
courtship duration (s)
experimental
control
type of male

CHAPTER V

Juvenile males prefer adult male tutors with high quality sexual displays

ABSTRACT

While the importance of adult male tutors for song learning in socially-monogamous songbirds is widely appreciated, the role of display trait tutors in species with lek-like mating systems remains unclear. This is despite the fact that these species have played a central role in our understanding of sexual selection. I propose that in species with lek-like mating systems, sexual selection may favor the evolution of juvenile males' tutor preferences that facilitate the acquisition of high quality sexual displays. To test this hypothesis, I experimentally-augmented adult male satin bowerbirds' displays, and evaluated juvenile male display trait acquisition behaviors. I found that juvenile males preferentially visited the bowers of males with augmented blue decorations, and that once at the bower, juvenile males preferred to observe the courtship displays of adult males with augmented blue decorations. I also found that the juvenile males preferentially observed adult males with high-intensity displays, which were most attractive to females in mate choice. Juvenile males' tutor preferences for blue decorations and display intensity parallel preferences that females use in mate choice. Having tutor preferences that are similar to female mate choice preferences may be adaptive because they facilitate the acquisition of displays that are particularly attractive to females.

INTRODUCTION

Tutor preferences are critical for directing how young males learn display in many songbirds (Catchpole & Slater 1995), and these preferences are predicted to reflect the needs of the individuals that are learning. For example, in socially monogamous passerines where adult males defend resource-based territories and use their song elements primarily in territorial interactions, juvenile males prefer to learn local songs from their fathers and territorial neighbors (Bohner 1983; Clayton 1987; Payne & Payne 1993; Beecher et al. 1994; Catchpole & Slater 1995; Margoliash 2002). However, in highly polygynous species where males use their displays primarily to attract females (Andersson 1994; Höglund & Alatalo 1995), intersexual selection on males to have displays that are highly attractive to females in mate choice may favor juvenile males that have tutor preferences that facilitate the acquisition of attractive display elements. Here I propose and test the 'attractive tutor hypothesis' which predicts that juvenile males prefer adult male tutors that are attractive to females. One way young males could discriminate among tutors that vary in attractiveness to females is to use the same traits in tutor choice that are used by females in mate choice.

To test the attractive tutor hypothesis, I experimentally manipulated adult male display traits, and monitored juvenile males' display acquisition behaviors in the satin bowerbird (*Ptilonorhynchus violaceus*). This polygynous species has a lek-like

mating system, where adult males have multiple display traits used by females in mate choice (Borgia 1985; Patricelli et al. 2002; Doucet & Montgomerie 2003; Coleman et al. 2004), male mating success is highly skewed, and young males learn their displays by observing adult males displaying (Collis & Borgia 1992, 1993; Maxwell et al. 2004).

Adult male satin bowerbirds build specialized stick structures, called bowers, where courtship and copulation take place (Marshall 1954; Borgia 1985). Males decorate the areas in front of their bowers with objects collected from the environment, and have strong preferences for blue objects (Marshall 1954; Borgia et al. 1987; Hunter & Dwyer 1997). Females use blue decorations as cues when deciding which males to visit for courtship (Coleman et al. 2004), and blue decorations calm females during males' intense behavioral displays (Patricelli et al. 2003). Females prefer males with many blue decorations and high intensity displays as mates (Borgia 1985; Patricelli et al. 2002; Coleman et al. 2004). Among males, blue decorations are strongly correlated with other male display traits that are used by females in mate choice (Borgia 1985; Doucet & Montgomerie 2003; Patricelli et al. 2003). Thus, the attractive tutor hypothesis posits that juvenile male satin bowerbirds use blue decorations as cues to discriminate among adult male tutors that differ in overall display quality, and attractiveness to females. To test this hypothesis I augmented the blue decorations at half of the twenty-eight adult males' bowers in a natural population of satin bowerbirds, and evaluated the effects on juvenile males' tutor preferences.

Juvenile male satin bowerbirds practice display behaviors for seven years prior to attaining adult male plumage (Vellenga 1980; Collis & Borgia 1992, 1993; Maxwell et al. 2004). During this time, juvenile males frequently visit adult males' bowers and receive courtships from the bower owners (Collis & Borgia 1992, 1993; Maxwell et al. 2004); these courtships are similar to courtships given to females (Collis & Borgia 1992, 1993). Because males show age-related improvement in display elements (Loffredo & Borgia 1986), male-male courtship has been interpreted as an adaptation for learning sexual displays (Collis & Borgia 1992, 1993). Juvenile males can choose which adult males' bowers to visit, and their behaviors at these bowers differ: each juvenile male must decide whether to receive courtship from the bower-owning adult, and then once engaged in courtship, must decide how long to remain. To evaluate whether the quality of adult males' displays affects these decisions, I augmented the blue decorations at half of the bowers in my population, monitored initial bower visits by juvenile males, and calculated the proportion of visits that involved male-male courtship. The attractive tutor hypothesis predicts that, (i) juvenile males prefer to visit the bowers of adult males with augmented blue decorations, (ii) juvenile males prefer to receive courtship from males with augmented blue decorations, and (iii) juvenile males remain longer in courtships with males with augmented blue decorations. Once engaged in courtship, juvenile males may use additional adult male display traits in decisions related to remaining in courtship. Thus, I evaluated the relationship between male-male courtship duration and adult male display intensity, a trait used by females in mate choice (Patricelli et al. 2002, 2003). The attractive tutor hypothesis posits that juvenile males prefer to

observe the displays of adult males that are attractive to females in mate choice. Thus, I evaluated the relationship between courtship duration and adult male mating success, a direct measure of male attractiveness. The attractive tutor hypothesis predicts a positive relationship between male-male courtship duration and display intensity, and courtship duration and adult male mating success.

METHODS

This study was conducted in 2000 in a natural population of satin bowerbirds at Wallaby Creek, NSW, Australia (Borgia 1985). From 1 September through 28 October, individuals were captured using baited traps and mist nets. Each bird was fitted with three plastic leg bands arranged in a unique color-combination and was categorized into sex and age groups by plumage (Vellenga 1980).

Throughout the mating season (1 November – 20 December), I monitored 28 adult males' bowers using an automated video monitoring system (for details see Borgia 1995). All individuals observed at bowers were identified on video footage from their unique color-band combinations. This marking and monitoring system allowed me to calculate adult male mating success (number of different mates) and to identify all juvenile male visitors and individuals engaged in male-male courtship.

In the decoration augmentation experiment, I paired bower-owning males (n = 14 pairs) based on mating success data from previous years and on the number of shared visiting females (see, Coleman et al. 2004). I used twenty blue plastic tiles

(2.54 cm x 2.54 cm) and 50 strands of blue plastic to augment the bower decorations of one male (the 'experimental male'), randomly chosen, in each pair. Decorations on 'control males'' bowers were unaugmented. Experimental males were allowed to place the tiles and plastic strands on their bower platforms. To prevent stealing by neighboring bower owners (Borgia & Gore 1986), I glued each tile to the head of long (7.62 cm) screw that was secured in the bower platform. Bower owners wove the plastic strands into their bower platforms. Twice daily I counted the numbers of tiles and plastic strands, and I replaced them to original levels as necessary. I removed tiles and plastic strands found on control males' bowers. Also twice daily, I counted the number of natural bower decorations at each bower. Experimental and control males did not differ in the mean number of natural decorations ($t_{26} = 1.35$, $P = 0.19$).

For each adult male, I calculated display intensity in the first courtship with each of the females he courted (for details on male-female courtships see, Coleman 2005). Using previously described methods (Patricelli et al. 2003), I calculated the intensity of each adult male's display based on three variables: (i) the distance run by the male during his display, (ii) the degree of the male's ptiloerection, and (iii) the location of the male on the bower platform. For use in statistical analyses, I calculated the mean display intensity for each adult male.

Using only a single point sample to measure an individual's preferences can be misleading. If the first adult male visited for courtship represents a juvenile male's 'tutor preference', then I predict that the first adult male visited for courtship is also the adult male most frequently visited for courtship. Indeed, for 30 of the 39 juvenile males I observed, the first male they visited was also the adult male visited most

frequently for subsequent courtships ($\chi^2 = 11.31$, d.f. = 1, $P < 0.001$). Thus, I am confident that the first adult male visited accurately reflects a juvenile male's tutor preference.

RESULTS AND DISCUSSION

The hypothesis that tutor attractiveness to females affects tutor preferences of young males has not been tested. I tested this hypothesis by augmenting some adult males' bowers with blue decorations, and then monitoring juvenile males' visits to experimental and control bowers. The attractive tutor hypothesis predicts that juvenile males prefer to visit, and receive courtship from, adult males with augmented decorations ('experimental males'). Twenty-six juvenile males first-visited experimental males' bowers, while 13 juvenile males first-visited control males' bowers ($\chi^2 = 4.33$, d.f. = 1, $P = 0.037$) (Fig. 1a). This result shows that juvenile males use blue decorations as cues to decide whether to visit adult males' bowers, and prefer to visit adults with highly decorated bowers. These preferences parallel those of female satin bowerbirds, who use blue decorations to decide whether to visit males' bowers during mate choice (Coleman et al. 2004).

Once at a bower, a juvenile male can choose whether to receive courtship from the bower owner; juvenile males frequently leave the bower area before the bower-owning adult male begins his courtship display (S. W. Coleman and G. Borgia in prep.). To test the prediction that juvenile males preferentially receive courtship

from males with augmented blue decorations, I calculated the proportions of initial visits that involved courtship at experimental and control males' bowers. Supporting the attractive tutor hypothesis, the mean proportion of initial visits to experimental males' bowers that involved courtship was greater than the mean proportion of visits to control males' bowers that involved courtship ($t_{26} = 2.46$, $P = 0.01$) (Fig. 1b). This result supports the hypothesis that juvenile males use adult males' blue decorations as cues for locating desirable adult males for courtship, and prefer to receive courtship from adults with high quality decoration displays. This use of blue decorations by juvenile males in tutor choice directly parallels the mate choice behaviors of female satin bowerbirds who use blue decorations to decide whether to receive courtship from males (Coleman et al. 2004).

Once adult males begin their courtship displays, juvenile males can decide how long to remain engaged in courtship. I can assess juvenile males' interest in adult males' displays by measuring courtship duration (juvenile males can terminate courtships at any time), thus the attractive tutor hypothesis predicts that juvenile males preferentially remain in courtships with adult males with augmented bower decorations. I was unable to support this prediction, finding that the decoration augmentation experiment had no effect on courtship duration ($t_{26} = -0.30$, $P = 0.76$).

My results suggest that juvenile males use blue decorations to choose tutors (Fig. 1a, b), but that once an adult male begins his courtship display, juvenile males' decisions to remain engaged in courtship are not affected by blue decorations. Instead, juvenile males may use other display elements to decide whether to remain engaged in courtship. Thus, I tested the hypothesis that tutor display intensity affects

male-male courtship duration. Female satin bowerbirds prefer adult males with the most intense displays as mates (Patricelli et al. 2002), thus the attractive tutor hypothesis predicts a positive relationship between male-male courtship duration and adult male display intensity. I found no difference in display intensity between experimental and control males ($t_{26} = 0.64$, $P = 0.53$), so I combined these groups for regression analyses. I found a positive relationship between adult male display intensity and male-male courtship duration ($r^2 = 0.17$, $F_{1,26} = 5.25$, $P = 0.03$) (Fig. 2). By choosing to remain in courtships with the most intensely-displaying tutors, juvenile males show a similar preference for a behavioral display trait that is used by females in mate choice (Patricelli et al. 2002; Coleman et al. 2004).

The hypothesis that juvenile males share preferences used in tutor choice that are expressed by females in mate choice predicts a positive relationship between adult male mating success (number of different mates) and male-male courtship duration. Supporting this prediction, I found that courtship duration was positively related to male mating success ($r^2 = 0.28$; $F_{1,26} = 10.06$; $P = 0.004$) (Fig. 3). This result shows that juvenile males choose to spend more time being courted by adult males that are preferred by females as mates. Having preferences that lead to preferential observations of the adult males that are attractive to females in mate choice may facilitate the acquisition of attractive displays.

An alternative hypothesis to explain the relationship between juvenile male tutor preferences and adult male display traits is that juvenile males follow females as they visit attractive adult males in mate choice. This hypothesis predicts a positive correlation between the frequency of bower visits by juvenile males and the

frequency of bower visits by mate searching females. I did not find support for this prediction; in fact, the relationship between the frequencies of male bower visits and female bower visits was negative (r_S = -0.84, P = 0.001), and the period of highest male bower visitation occurred approximately 30 days before the period of highest female bower visitation (Fig. 4). Thus, it is unlikely that juvenile males gain information on tutor attractiveness by following female mate searching behaviors.

Another alternative hypothesis is that juvenile males have a sensory bias for the color blue, and thus are attracted to adult males with many blue decorations. This hypothesis seems unlikely for two reasons. First, in an experiment where I gave males choices of different colored decorations, I found that first-, second-, and third-year males preferred green decorations over blue decorations, while older males preferred blue decorations over all other colors (S. W. Coleman unpub. data). Second, the sensory bias hypothesis predicts that male satin bowerbird visual systems bias their preferences for blue objects – perhaps through spectral tuning of short-wavelength sensitive photoreceptors. This is not the case: the sensitivities of male satin bowerbird photoreceptors, and the distribution of photoreceptors on the retina, are typical of many forest-dwelling passerines (J. Marshall pers. comm). Thus, there is little support for the sensory bias hypothesis.

There is evidence from many species that traits that affect female choice are learned (Bohner 1983; Clayton 1987; Collis & Borgia 1992, 1993; Payne & Payne 1993; Beecher et al. 1994; Catchpole & Slater, 1995; Langmore 1999; Margoliash 2002; Maxwell et al. 2004). Models of learning predict that individuals should be highly selective when choosing from whom to learn sexual displays (Laland 2004).

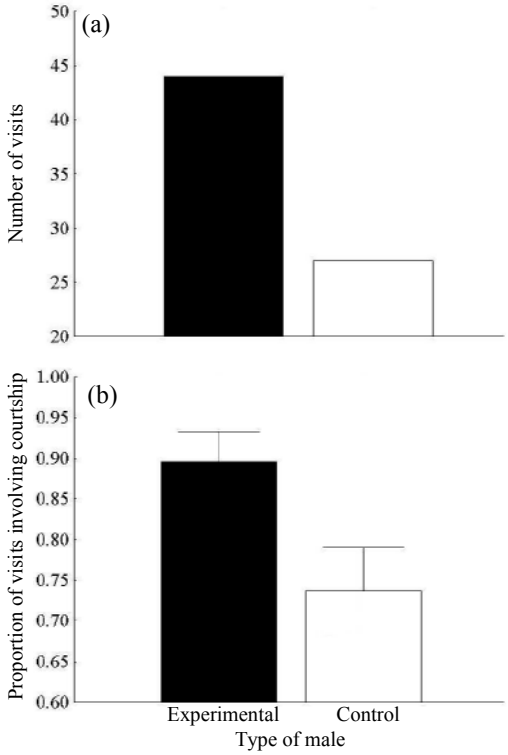
My results support this prediction, and suggest that juvenile male satin bowerbirds choose display trait tutors in an adaptive way; that is, they choose tutors with traits that are attractive to females. I show that juvenile males use blue decorations to decide which adult males to visit and receive courtship from, but then focus on tutors' behavioral display elements, such as display intensity, to decide how long to remain engaged in courtship. Female satin bowerbirds use a similar process when choosing their mates: females use blue decorations to decide which males to visit and which males to receive courtship from, but once engaged in courtship, most females emphasize male display intensity in their mate choice decisions (Coleman et al. 2004). The similarity in the use of adult male display traits between females and juvenile males indicates that juvenile males have tutor preferences that are similar to female mate preferences. This is the first study to identify the cues underlying tutor discrimination in a species with a non-resource based mating system, and to show that young males have evolved adaptive tutor preferences that are similar to female preferences used in mate choice.

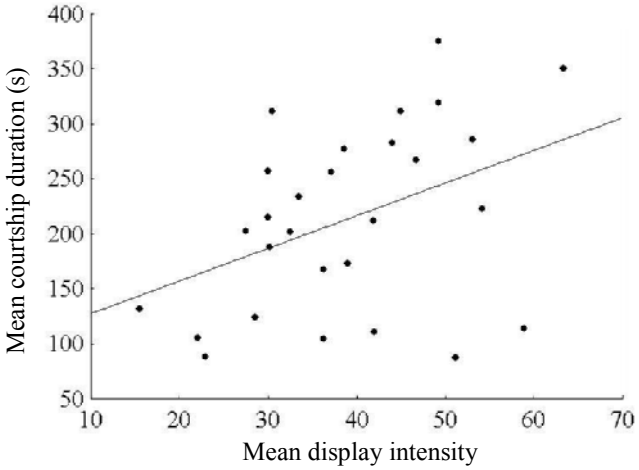
Figure 1. Comparisons between (a) the numbers of juvenile males observed visiting experimental males' bowers versus control males' bowers, and (b) the proportions (mean + SE) of those visits in which juvenile males were courted by bower-owning adult males. This figure shows that juvenile males prefer to visit, and receive courtship from, adult males with the most attractive decoration displays. Female satin bowerbirds use blue decorations to decide which males to visit for courtship (Coleman et al. 2004), and prefer males with the most blue decorations as mates (Borgia 1985; Coleman et al. 2004).

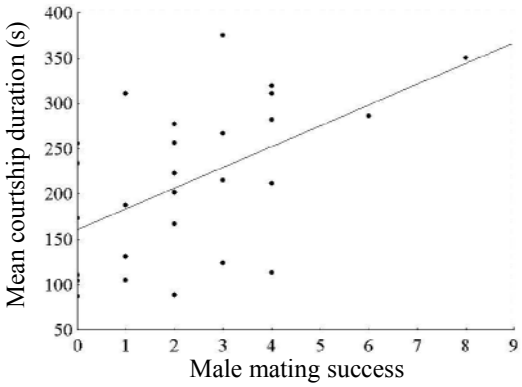
Figure 2. Scatterplot showing the relationship between male-male courtship duration and adult male display intensity. The relationship indicates that juvenile males prefer to remain engaged in courtship with the adult males that have the most intense displays. These preferences parallel those of female satin bowerbirds who prefer the most intensely-displaying adult males as mates (Patricelli et al. 2002).

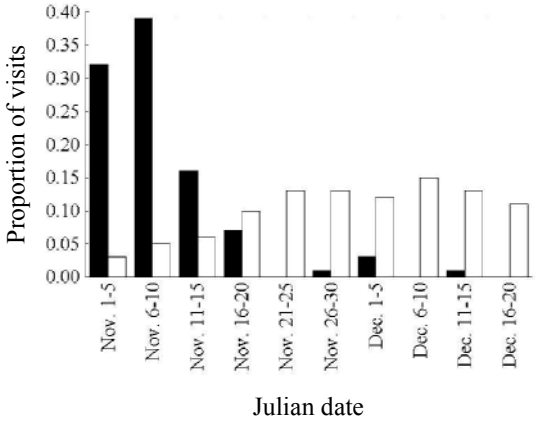
Figure 3. Scatterplot showing the relationship between male-male courtship duration and adult male mating success. This figure indicates that during male-male courtship, juvenile males assess adult males' displays, and choose to remain engaged in courtship with the males whose displays are most attractive to females in mate choice. The relationship remains positive and significant even after removing the two top males (mating success = 6 and 8) ($r^2 = 0.17$, $F_{1,24} = 4.85$, $P = 0.03$).

Figure 4. Bar graph showing the relationship between Julian date and the proportions of tutor-related visits by juvenile males (solid bars) and the proportions of mate assessment visits by females (open bars). This figure shows that it is unlikely that juvenile males use information from mate searching females to identify attractive adult male tutors.


(a)
Number of visits
50
45
40
35
30
25
20
(b)
Proportion of visits involving courtship
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
Experimental
Control
Type of male


Mean courtship duration (s)
400
350
300
250
200
150
100
50
10
20
30
40
50
60
70
Mean display intensity


Mean courtship duration (s)
400
350
300
250
200
150
100
50
0
1
2
3
4
5
6
7
8
9
Male mating success


Proportion of visits
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Nov. 1-5
Nov. 6-10
Nov. 11-15
Nov. 16-20
Nov. 21-25
Nov. 26-30
Dec. 1-5
Dec. 6-10
Dec. 11-15
Dec. 16-20
Julian date

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